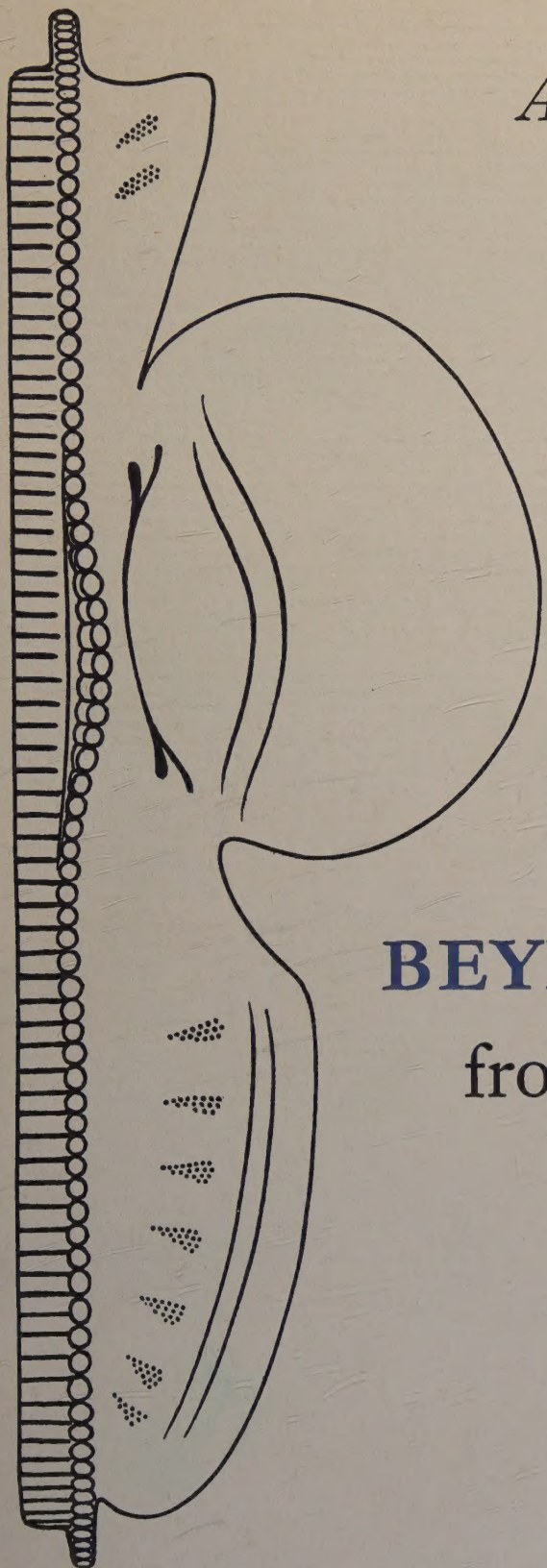
Anders Martinsson



Ostracodes of the Family BEYRICHIIDAE from the Silurian of Gotland

UPPSALA 1962

OSTRACODES OF THE FAMILY

BEYRICHIIDAE

FROM THE SILURIAN OF GOTLAND

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OSTRACODES OF THE FAMILY BEYRICHIIDAE FROM THE SILURIAN OF GOTLAND

BY

ANDERS MARTINSSON

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Ostracodes of the Family Beyrichiidae from the Silurian of Gotland

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ABSTRACT.—The present paper deals with the morphology, phylogeny and systematics of the palaeocope ostracode family *Beyrichiidae* MATTHEW 1886 as illustrated by material from previously very little known faunas from the Silurian sequence of the Isle of Gotland, Sweden. This study is divided into three main parts to which an appendix, discussing the most recent papers, has been added.

(1) An historical review of those earlier studies which lead up to the present views of the family *Beyrichiidae* is given. The original material of most species which have been or could be expected to be considered in the treatment of the faunas from Gotland has been traced and refigured. This section treats material from Gotland, Scania, Britain, and from erratics in Northern Germany and also includes most of the material earlier regarded as lost as a result of the Second World War. Lectotype and neotype designations are made in digressions from the historical text.

In this part, also, methods for the treatment of Palaeozoic ostracodes in marly deposits, largely developments or simplifications of earlier known methods, are discussed. A method of manual needle preparation of objects attached to a film of cellulose acetate in water immersion (for special purposes two kinds of films soluble in different solvents are used) is described.

The distribution of beyrichiid species in the sequence of Gotland is reviewed with current stratigraphical conceptions of the local Silurian sequence as a background.

(2) A systematic survey of the surface morphology and terminology is made before certain trends in the development of lobal, adventral, and ornamental structures are analysed from ontogenetic and phylogenetic points of view.

The beyrichiid larvae hatched already in the typical beyrichiid brood pouch, the crumina. They passed through nine moult stages before death, approximately doubling their volume in each moulting. Biometric analyses of especially the very stable ecodeme from Mulde demonstrates the size grouping of the moults very distinctly.

In the eight first stages all specimens gradually develop towards the shape of the adult males (*tecnomorphs*). The sex ratio of beyrichiids investigated is 50:50. During the last moulting 50 per cent of the adult specimens (*heteromorphs*; i.e. adult females) undergo the *cruminal metamorphosis* which is not anticipated in the penultimate moult stage and is completed before the last stage is calcified. In one of thousands of heteromorphs the metamorphosis is interrupted before completion, and atavisms in the classic sense are obtained.

It has been suggested earlier that the beyrichiids were more or less direct descendants of eurychilinaceans which developed a pouch anteroventrally in the velum, and the genus *Chilobolbina* has been pointed out as a transitional form.

Both certain *Eurychilinacea* and atavistic *Beyrichiidae* developed a pouch by forming a bulge, a *dolon*, anteroventrally in a broad, tubulous, frill-like velum; the cavity within this bulge opens externally. The ontogenetic evidence strongly corroborates a descendence of the *Beyrichiidae* —whose crumina opens internally, towards the main space (domicilium) of the carapace—from eurychilinacean-like ancestors. The phylogenetic development of cruminate ostracodes, however, as illustrated by phylogenetic as well as the new ontogenetic evidence, has taken place along lines quite different from those hitherto assumed.

The dolonate beyrichiacean ancestors developed a semiglobular dolonal pouch anteriorly in the velum of each valve; the edges of the pouches were probably not in contact, as is the case in *Chilobolbina*. The dolonal part of the velar edge was extended into a flap more or less covering the opening of the dolonal space and finally inserted behind the proximal part of the margin of this opening. Probably already in connection with this, the velar tubules, opening towards the domicilium during an early stage of the moulting, were invaded and extended into a cruminoid space which tended, however, as all other tubules, to become closed and separated from the

domicilium; the cruminal opening originated in primitive beyrichiids by secondary perforation of the closing tissue.

These conditions are traced in atavistic specimens of the new subfamily *Craspedobolbininae*, and the development was repeated in the ontogeny of the craspedobolbinines. Less primitive beyrichiids tended to suppress the dolonoid mechanism, to invade the tubules of the velar fold more directly, and to incorporate considerable parts of the carapace wall with the crumina. Thus the *Treposellinae* had originally an anteroventral crumina which is in most forms only the anterior end of a voluminous, mainly posteroventral, cruminal swelling. The *Amphitoxotidinae* abandoned the dolonoid stage and invaded a primitively constructed velum more or less completely, inflating it and relatively minor parts of the carapace wall into a sphaeroidal crumina. The *Zygobolbinae* incorporated considerable parts of the carapace wall elements with the crumina but retained the traces of the dolonoid mechanism as a characteristic plication breaking the edge of the valve. The *Beyrichiinae* developed along similar lines but have no dolonoid scar, though the edge of the valve is often somewhat affected. The *Kloedeniinae* (not occurring on Gotland; to be treated in detail in a forthcoming paper) reduced the velum into a fairly obtuse bend which was inflated into a crumina in the adult female. In some beyrichiids, as in the isolated *Hexophthalmoidinae*, the cruminal metamorphosis cannot be traced in this way.

(3) Partly as a background for the discussion on the developmental trends within the family, partly as a framework for future stratigraphical work with the microfaunas of Gotland, the abundant *Beyrichiidae* in the Silurian sequence of this island are described. Some forms from other areas which illustrate special developmental lines (e.g. in *Apatobolbina*, Wenlockian *Amphitoxotidinae*, Devonian *Treposellinae*, and *Zygobolbinae*) are also taken up for more detailed treatment. The new subfamilies *Craspedobolbininae*, *Amphitoxotidinae*, and *Hexophthalmoidinae* are introduced. The more detailed treatment comprises 44 genera, three of which are divided into 12 subgenera in all; 31 of the genera and 7 of the subgenera are new. Of the 127 species treated to a corresponding extent 97 are new; 114 beyrichiid species occur on Gotland (there are, at least, 6 more species in the material from Gotland which are not described owing to lack of material). *Nomenclatura aperta* is used for 13 (14) of these species. The names of taxia treated are found in systematical order in the following Table of Contents.

A certain homoeomorphy in the lobation is found in different subfamilies which has led earlier systematics to cut across the natural lines of development and unite representatives with similar lobation but belonging to different subfamilies in the same genera, such as *Neobeyrichia* and *Craspedobolbina*. A genus which has very unexpectedly proved to belong to the beyrichiids, is *Strepula*.

The systematic position of the *Beyrichiacea* as illustrated by the new phylogenetic and systematic views is discussed in a survey of the suborder *Palaeocopa*.

(4) The conceptions of the morphology of the *Beyrichiidae* presented in the ostracode part of the "Treatise on Invertebrate Paleontology", which are partly new and partly considerably divergent from views presented in this paper, are discussed in an Addendum.

Abbreviations of depositories

Original numbers referring to collections in Sweden may be recognized by the following index letters:

Series *G*, *Sk*, *WE*, and *NA*: Institute of Palaeontology, University of Uppsala (regional collections).

Series *Ar*: Department of Palaeozoology, Swedish State Museum of Natural History, Stockholm (Naturhistoriska riksmuseet, abbreviated *RM*; arthropod collections).

For specimens deposited in other countries the name of the museum is repeated in each case.

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INTRODUCTORY PART

General introduction

The present paper is intended to be the first in a series dealing with certain groups of microfossils from the Silurian strata of Gotland. It has been preceded by a number of preliminary studies which have proved the relative abundance right through the sequence of various microfossils, especially of ostracodes in the marls. Among the ostracodes, the highly specialized suborder *Palaeocopa*, represented mainly by the families *Beyrichiidae*, *Primitiopsidae*, and *Hollinidae*, all characterized by their sexual dimorphism, has been of special interest. After some years' washing and extraction of the material it gradually became evident that it would be unreasonable to treat even the three ostracode families mentioned above in a common paper, and therefore the investigation has been concentrated primarily to the most differentiated of them, the *Beyrichiidae*.

The object of this part of the investigation was originally to provide a taxionomical survey of the beyrichiid ostracodes which can be used as a basis for future stratigraphical work, especially on subsurface material, in the Silurian of Gotland, but as the phylogenetic and systematic aspects of the family gradually became a main theme of the study, its descriptive parts have acquired rather the character of a background illustration of the phylogenetic lines and the abundance of forms within the family. This has required the inclusion of some forms from areas outside Gotland, partly in anticipation of forthcoming studies. The material, however, is excellent for several other kinds of investigations, e.g. ecological, microstructural, and biostatistical ones, but unless they contribute directly or substantially to the attainment of the object defined above they have not been taken up here. In some instances, nevertheless, interesting by-products have appeared during the study and are added as digressions or notes. As noted in the following some isolated problems have been or are being taken up for more extensive study than could reasonably be included in the present publication.

It is evident from the definition given above and from the fact that only one family of several larger macro- and microfossil groups is taken up for discussion, that this study alone is no basis for a review or revision of the Silurian sequence of Gotland. As, however, the collecting localities and the stratigraphical distribution of the ostracodes are to be stated, it is impossible to avoid taking up the present views on the stratigraphy of Gotland for a short presentation.

It is necessary to stress another limitation of this study. The new material involved comes exclusively from marly facies, marl pockets in the reefs, or

from marly intercalations in the bedded limestones. Subsurface material and specimens obtained from limestone matrix are consequently excluded, though they have been used for some controls. This limitation would be expected to lead to a biofacial specialization which would exclude many important forms from being studied. As far as checks have been made these fears have not been corroborated. The composition of the limestone faunas agrees well qualitatively, if not quantitatively, with that of the corresponding marl faunas, and in the light of the millions of ostracodes picked out it is very probable that occasional stenoecic guests from limestone-forming facies would also be included in the marl faunas.

The reason for this concentration to the marly facies is the need for an abundant material, or at least material of both dimorphs, for the description of a species; the material should also be capable of being prepared in such a way that the morphological details essential for a taxionomic treatment can be observed and studied. As demonstrated in the following it is often indispensable for the primary description of a taxion to have access to the ventral side of the specimens. Too many types and type species of fossil ostracodes consist of young moult stages or specimens so firmly adherent to the matrix that the critical parts cannot be exposed; still worse is the case when the types consist of internal or external moulds. These demands on the description do not, of course, prevent an already described ostracode species from being recognized even if it is largely buried in a limestone and represented only by a young moult stage.

When treating an organism group taxionomically the knowledge of the phylogenetic relationships within the group and its affinities to other groups is of major importance. It is natural, therefore, that large parts of the present paper deal with phylogenetic aspects on the beyrichiids and type revisions or discussions of ostracodes which are not represented on Gotland.

Experience has shown that, with the exception of some relatively recent papers with good photographical illustrations, it is practically impossible to work systematically on palaeocopes on the basis of figures given in publications. In so far as types and other originals of crucial importance have been accessible they have been revised here. These revisions, however, have been limited by the fact that some originals cannot be traced, have been destroyed as a result of the war, or are not sent out on loan by the museums in which they are deposited.

The results of this investigation already published in preliminary reports (Martinsson 1955, 1956, and 1960b) are included entirely or partly in this treatise, and a number of illustrations from them, essential for the reader's reference, are reprinted here.

Acknowledgements.—This investigation was entirely carried out under the auspices of the Institute of Palaeontology, and I heartily thank its Director, Professor P. Thorslund, for his continuous and generous readiness in securing the grants which have

financed the laboratory work and in authorizing the adaption of considerable parts of the Institute, its instrument equipment, and library accession to the needs of the growing micropalaeontological activity within the Institute.

It has been a great asset to have a colleague at the Institute working on the Middle Ordovician palaeocopes and on the main problems in palaeocope systematics, and sincere thanks are due to Dr. VALDAR JAANUSSON for years of discussion and cooperation.

For grants defraying the costs of the field work, journeys, and some of the instruments I am indebted to the LILJEWALCH, OTTERBORG and BJURZON Funds, the Funds of the Faculty of Science of the University of Uppsala, the GUSTAF LINDSTRÖM Memorial Fund and the TH. NORDSTRÖM Fund, both of the Royal Swedish Academy of Science, and for part of the printing costs to the Council for Research in Natural Sciences.

I have had the great advantage of the learned guidance and company, on several excursions to Gotland, of Dr. J. E. HEDE, Lund, on whose works the present concepts of the stratigraphy of Gotland are founded. The companionship in the field of Dr. A. J. BOUCOT on Gotland, Dr. A. URBANEK in Poland, Dr. H. JAEGER in Germany, and Drs. J. D. LAWSON, V. G. WALMSLEY, and J. MCD. WHITAKER in the Welsh Borderland has been of direct importance for this study.

For the loan of specimens I am indebted to the authorities of the following museums and to the following officials arranging the loans: The British Museum (Natural History), London, through Dr. W. T. DEAN; the Geological-Palaeontological Museum of the HUMBOLDT University, Berlin, through Professor W. GROSS, Dr. K. DIEBEL, and Dr. H. JAEGER; the District Museum of Neubrandenburg through Drs. LUCKOW and G. STEINICH; the Palaeontological Museum of the University of Oslo through Dr. G. HENNINGSMOEN; the U.S. National Museum through Dr. G. A. COOPER, Dr. R. S. BOARDMAN, and Dr. JEAN M. BERDAN; and the State Museum of Natural History, Stockholm, through Professors E. STENSIÖ and E. JARVIK, and Dr. H. MUTVEI.

By far the larger part of the time used for this investigation has been taken up by the routine work of washing and extracting millions of ostracodes. During the last few years I have had temporary aid in this from students and occasional employees whom I wish to thank, especially mentioning Mr. H. GODBERG's major contribution. Thanks are also due to the ordinary staff of the Institute: to Mrs. EVA EKLIND (preparation for publication of the manuscript), Mrs. MEIT LINDELL (laboratory work), Mrs. INGA THOMASSON (diagrams), Mr. N. HJORTH (darkroom work), and Mr. E. STÅHL (drawings).

Historical survey and type revisions

This historical survey concentrates upon such investigations as lead more or less directly up to the present one, and more peripheral papers will be given very little attention. It includes the identifications of those originals which are of particular interest with respect to taxia represented in the faunas of Gotland. As far as it has been possible to identify the originals to be designated as types they are figured in the original state of representation, or, mostly, after preparation. The documentary interest and the possibilities of preparation have been decisive for the choice in each case. In some instances early writers have figured details in the matrix with more accuracy than the animal itself.

The history of the discovery of fossil beyrichiid ostracodes has been summarized by early writers (e.g. JONES 1855a, BOLL 1862, KOLMODIN 1869, and JONES and HOLL 1886a). First to figure them was C. F. WILCKENS in 1769,

in an illustration together with trilobites determined as *Agnostus pisiformis*, but he could not reach any definite conclusion on their place in the system; the species figured was probably *Kloedenia wilckensiana* (*fide* JONES 1855a, pp. 82 and 90). L. VON BUCH (1828 and 1831) commented and figured beyrichiids but regarded them as young stages of the brachiopod *Leptaena lata*. KLÖDEN (1834) referred them to the agnostid trilobites again, and BURMEISTER (1843) believed them to be odontopleurid trilobites. All material mentioned hitherto came from glacial erratics in northern Germany. Though their Late Silurian age gradually became clear, the confusion with Upper Cambrian trilobites led to such stratigraphical confusions as those still found in JONES (1855a, p. 82).

KLÖDEN's *Battus tuberculatus* of 1834 is the first beyrichiid species named. KLÖDEN gave a series of more or less naturalistic figures of more or less certain beyrichiids, but it is almost certain that at least one of them, Fig. 21a–b, is identical with the species traditionally named *Beyrichia tuberculata* which KESLING & WAGNER (1956) have made one of the best figured beyrichiids in literature. It is beyond all doubt, however, that this *Neobeyrichia* (*Nodibeyrichia*) species is not identical with *Beyrichia kloedeni* M'COY as suggested by KESLING & WAGNER (1956) which would have had as a consequence that the genus *Beyrichia sensu stricto* would have comprised quite another genus of beyrichiids than after HENNINGSMOEN's revision (1954; cf. MARTINSSON 1960c and below).

In 1845 BEYRICH recognized the beyrichiids as ostracodes, and in 1846 M'COY became the author of the first generic name given to these animals, *Beyrichia*. The type material of his species, *B. kloedeni*, consists of moulds in the Upper Llandoverian sandstones of Boocaun and the slates of Capparcorcogue, Cong, County Galway, Ireland, and has been examined by STRAW (1928), who figured two internal moulds showing the general outline and lobation, and by HENNINGSMOEN (1954, p. 23) who adds important information about the tuberculation along the velar ridge and on the existence of a faint syllobial groove. As discussed by MARTINSSON (1960c) there can be no doubt that this species is different from *Battus tuberculatus* KLÖDEN, and after the paper last quoted was written in 1958 it has become fully evident that the most distinct of KLÖDEN's figures, No. 21a, which has served as a basis for later identifications of *B. tuberculata sensu stricto*, represents a much younger species than *B. kloedeni*, younger than any strata represented on Gotland. According to present taxionomy they even belong to different genera, *Beyrichia* (*Beyrichia*) and *Neobeyrichia* (*Nodibeyrichia*), respectively. The species most closely related to *B. kloedeni* known in well-preserved conditions, possibly even identical with it, is the species in Fig. 1, from the Wenlock Limestone of the Welsh Borderland, included in *B. kloedeni* var. *tuberculata* SALTER as determined by JONES and HOLL (1886a, p. 355).

VON EICHWALD (1854) described an ostracode from Gotland (cf. D'EICHWALD 1860, p. 1346) under the name of *Beyrichia Retzii*. It was without doubt a

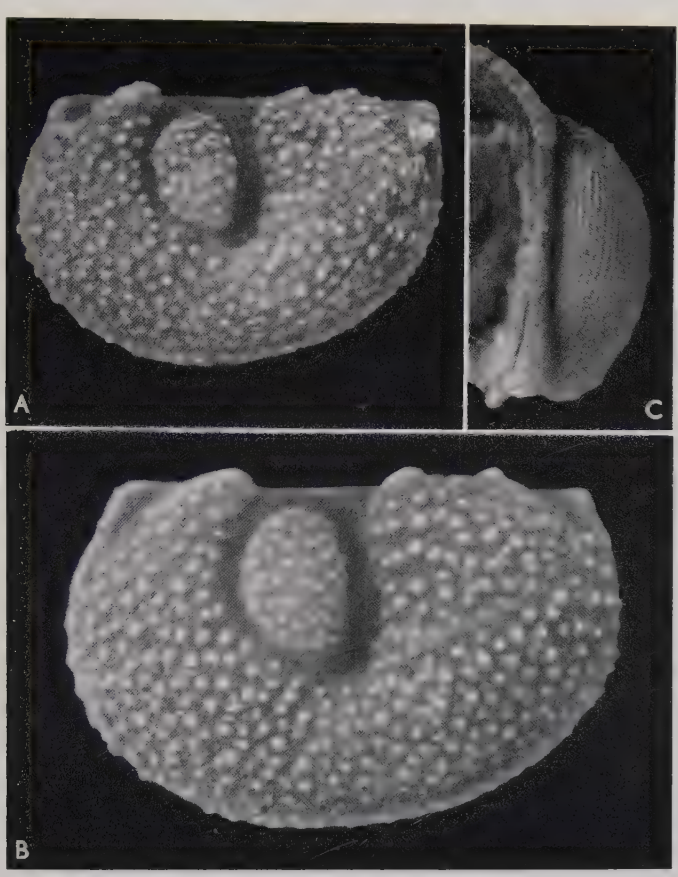


Fig. 1. *Beyrichia* (*Beyrichia*) cf. *kloedeni* (M'Coy). Shropshire, Gleedon Hill Quarry N of Much Wenlock. Wenlock Limestone; upper part of the section exposed. A. Young tecnomorphic carapace, No. EW 1. B. Male carapace, No. EW 2. C. Fragmentary left female valve, ventral side of the crumina, No. EW 3. Anterior end up. A–C × 30. Cf. text, pp. 14 and 269.

beyrichiid; as described, and lacking a figure, it can only be regarded as a *nomen dubium*.

In 1855 the knowledge of beyrichiids was considerably increased by two papers by Jones (1855a and b), and in the same year N. P. Angelin prepared his "Tabula A", intended to accompany a third fascicle of the "Palaeontologia Scandinavica", illustrating numerous ostracodes from Gotland, among them beyrichiids with male and female specimens correlated with each other.

The first mentioned of Jones's papers (1855a) contains descriptions of the faunas in five erratic boulders from Prussia ("near Berlin") and Silesia ("near Breslau"), containing a number of species which are among those most frequently mentioned in literature concerning Gotland and the Baltic area. He further subdivided the genus *Beyrichia*, which he tentatively referred to the Phyllopoda and in which he also placed a number of non-beyrichiid ostracodes

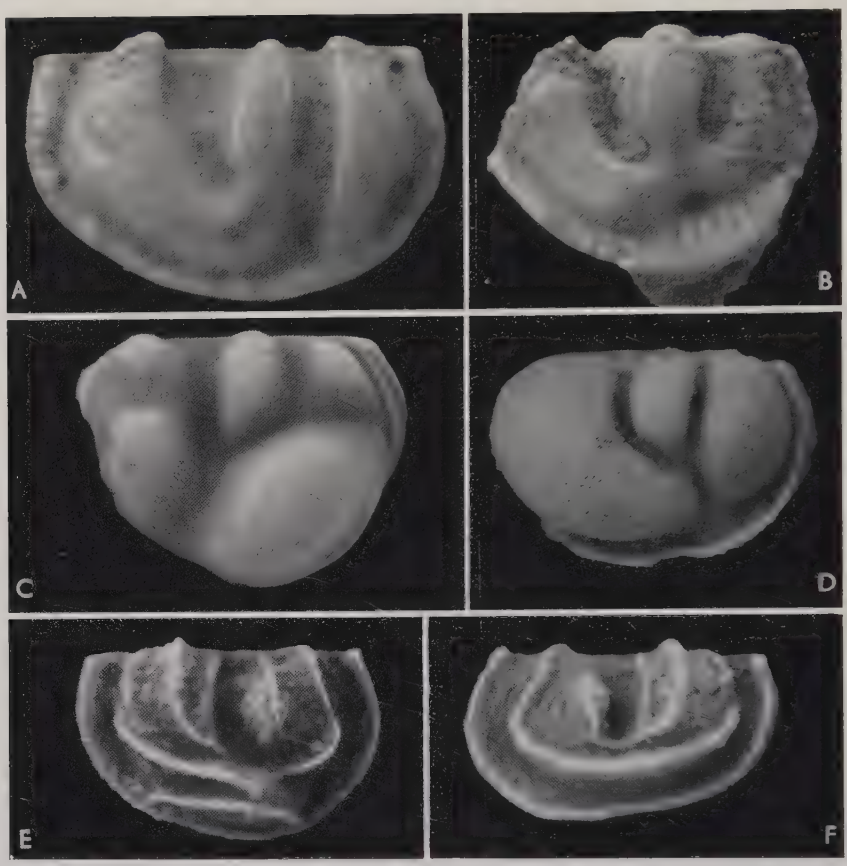


Fig. 2. A. *Neobeyrichia* (*Neobeyrichia*) *buchiana* (Jones 1855), lectotype of *Beyrichia Buchiana* Jones 1855. × 30. B. *Hemsiella maccoyiana* (Jones 1855), lectotype of *Beyrichia Maccoyiana* Jones 1855. × 30. C. *Hemsiella dalmaniana* (Jones 1855), lectotype of *Beyrichia Dalmaniana* Jones 1855. × 30. D. *Macrypsilon salterianum* (Jones 1855), lectotype of *Beyrichia Salteriana* Jones 1855. × 50. E. *Strepula concentrica* Jones & Holl 1886, lectotype of *Strepula irregularis* Jones & Holl 1886; right female valve. × 30. F. *Strepula concentrica* Jones & Holl 1886, lectotype of *S. concentrica* Jones & Holl 1886 (synonymous with *S. irregularis*). Male carapace. × 30. All in the British Museum (Natural History).

not further commented here, into three groups: *Simplices*, *Corrugatae*, and *Jugosae*. These names are not constructed as valid names in zoological nomenclature, but they have appeared again as arguments for attributing the family authorship of the *Beyrichiidae* to Jones (Kesling and Rogers 1957, pp. 998–999). The main arguments for this were, in addition, based on the facts that Jones, according to the usage of that time, used the plural, *Beyrichiae*, of the generic name in the text (as was the case in German and Swedish, too, with "*Beyrichien*" and "*beyrichior*", respectively), and that Matthew (1886) omitted the last *i* of the stem before the subfamily ending. Jones clearly stated that he regarded *Beyrichia* as a genus and placed it in a family, *Limnadiadae?*,

which further stresses the infrageneric character of these groups. As pointed out earlier (MARTINSSON 1960c) there is no formal possibility of altering the authorship of the family, and it is rather difficult to see why it should be desirable.

The originals of four of JONES's new species are refigured here in Fig. 2. The following lectotypes (Fig. 2) are designated here (originals in the British Museum [Natural History]):

Beyrichia Buchiana JONES 1855, No. I 6894, a right tecnomorphic valve (Fig. 2A), well preserved, weathered white, figured by JONES 1855a, Pl. V, fig. 1, from boulder No. 1, near Berlin. Other specimens of this species from the same boulder are Nos. I 6883–6888 and I 6900; the left valve figured by JONES in Pl. V, fig. 2 is No. I 6909. The matrix of No. I 6900 also contains *Kloedenia wilckensiana* (JONES).

Beyrichia Salteriana JONES 1855, No. I 7100, a right tecnomorphic valve (Fig. 2D), well preserved, agreing with JONES's Pl. V, fig. 15a, but not demonstrably identical with the original, from boulder No. 5, near Breslau. Other specimens of this species from the same boulder are Nos. I 7096 and 7097.—Attention is drawn to the dimorphism in this species by KESLING & ROGERS (1957, Pl. 128, figs. 14–17).

Beyrichia Dalmaniana JONES 1855, No. I 7019, a right female valve (Fig. 2C) with well preserved ornamentation, not identical with the specimen figured by JONES in Pl. V, fig. 13 (which cannot be identified), but mentioned on p. 88 together with this specimen, both from boulder No. 3 (near Breslau), as confirmed by label.

Beyrichia Maccoyiana JONES 1855, No. I 6953, a larger fragment of a right tecnomorphic valve (Fig. 2B), badly weathered, figured as a restoration in JONES's Pl. V, fig. 14, the only specimen obtained from boulder No. 2 (near Berlin) as confirmed by label. The two specimens mentioned by JONES on p. 89 from boulder No. 3 have not been identified and, according to the concomitant fauna, were less likely conspecific with *B. Maccoyiana*. The lectotype is not very attractive as a systematic key specimen, but the material from erratic boulders of this and related species is so representative that it will probably be possible to establish it as a good species.

Unfortunately no cotype material of *B. Wilckensiana* JONES 1855 could be found in these collections made by LYELL. The dubious *B. Wilckensiana* var. *plicata* JONES, however, is represented by Nos. I 6918–6921. As JONES's figure even gives information about the ventral morphology of the crumina (Pl. V, fig. 18b) there is no doubt as to the identity of the proper *B. Wilckensiana*, later type species of *Kloedenia*, and the reader is referred to KESLING's (KESLING 1956 b, Pl. VII) excellent figures of the species.

In the other paper JONES (1855b, Pl. VI, fig. 24) figured the first treposelline under the name of *Beyrichia seminulum* n.sp.

ANGELIN's plate A of 1855, illustrating ostracodes from Gotland, was distributed to colleagues abroad but was never included in a publication. As shown by WESTERGÅRD (1910, p. 5) the plates received wide attention, but it seems to have escaped notice that the figures were used as reference for several of JONES's identifications of ostracodes of Gotland (1887 and 1888a). It is interesting to note that ANGELIN consistently figured male and female specimens of the same species together.

In 1856 BOLL published a letter to BEYRICH with the descriptions of three new species, belonging to three genera of different subfamilies in the system

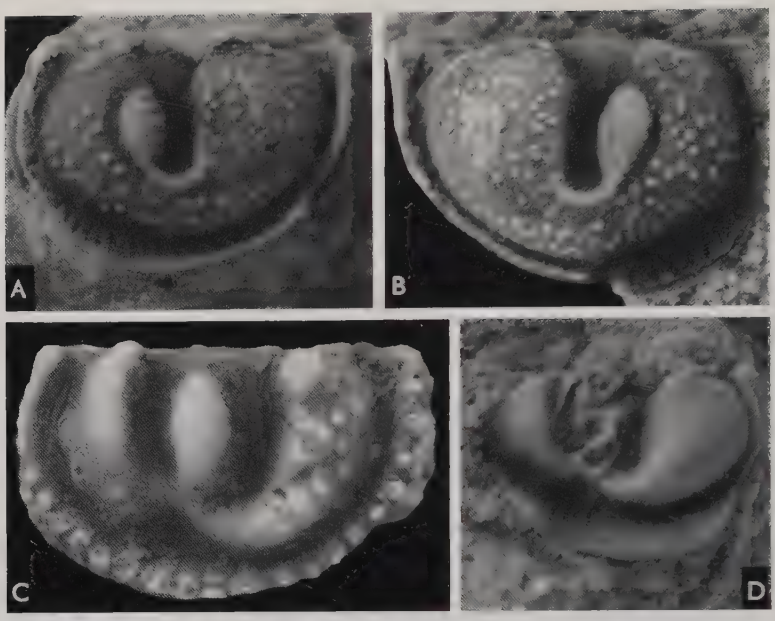


Fig. 3. A. Original of *Beyrichia Jonesii* Boll 1856, Fig. 1 (refigured by Boll 1862, Pl. I, fig. 8 and Kiesow 1888, Pl. II, fig. 10). ×30. B. *Craspedobolbina* (*Mitrobeyrichia*) *jonesi* (Boll 1856), lectotype of *Beyrichia Jonesii* Boll 1856 (refigured by Kiesow 1888, Pl. II, fig. 11). C. *Neobeyrichia* (*Neobeyrichia*) *spinulosa* (Boll 1856), lectotype of *Beyrichia spinulosa* Boll 1856 (refigured as *B. nodulosa*, an objective synonym, by Boll 1862, Pl. I, fig. 6 — *errore* also *B. spinosa*, op. cit., p. 131 — and by Krause 1891, Pl. XXXII, fig. 11). ×30. D. *Hemsiella hians* (Boll 1856), lectotype of *Beyrichia hians* Boll 1856 (probably refigured by Boll 1862, Pl. I, fig. 11). ×30. All in Heimatmuseum Neubrandenburg.

presented here. One of them, *Beyrichia Jonesii*, is one of the most frequently mentioned beyrichiid species—though it is doubtful if it has ever been identified since the description—and *B. spinulosa* and *B. hians* have also been referred to more or less frequently (cf. Bassler and Kellet 1934; the latter species is found with three references under *B. maccoyana*, p. 199).

The originals have long been regarded as lost. *B. Jonesii* is of particular interest as it was later made the type species of the subgenus *Beyrichia* (*Mitrobeyrichia*) Henningsmoen 1954. Kiesow (1888, Pl. II, figs. 10 and 11) figured naturalistically Boll's two specimens with the damages in the velum. A note in Kiesow's paper (op. cit., p. 2) made it probable that the specimens could be found in the Heimatmuseum der Stadt Neubrandenburg in the Treptower Torturm, Neubrandenburg. Boll's collection had suffered severe damage during the war, but Dr. G. Steinich succeeded in finding all originals of 1856. All specimens are refigured here, and the following lectotypes are selected (Fig. 3):

Beyrichia Jonesii Boll 1856, the right tecnomorphic valve (Fig. 3 B) figured by Boll in Fig. 1 on p. 322 and by Kiesow (1888) in Pl. II, fig. 11. It was found together with the other specimen figured by Boll (refigured by him 1862, Pl. I. fig. 8) and Kiesow

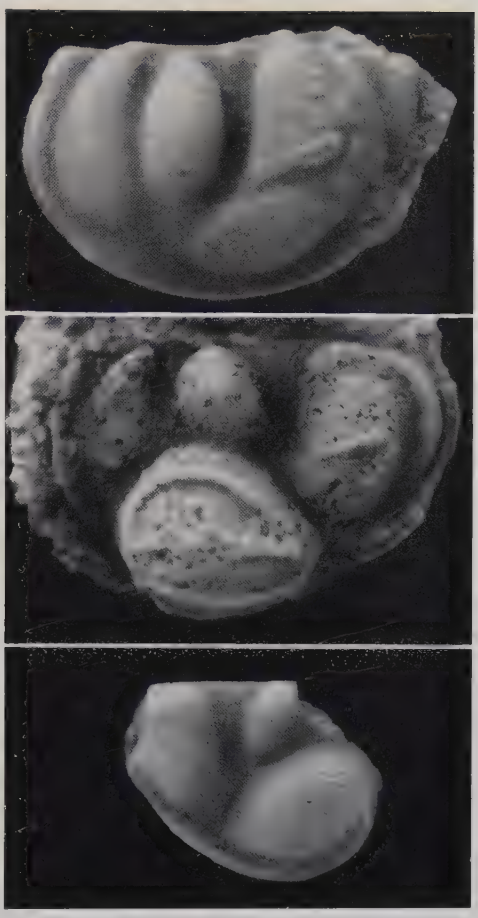


Fig. 4 A. *Sleia kochi* (BOLL 1862), lectotype of *Beyrichia Kochii* BOLL 1862. × 30.

Fig. 4 B. *? Sleia cincta* (BOLL 1862), lectotype of *Beyrichia cincta* BOLL 1862. × 30.

Fig. 4 C. *Hemsiella elegans* (BOLL 1862), lectotype of *Beyrichia elegans* BOLL 1862. × 30.

Fig. 4. Originals of figures published by BOLL 1862. All in Heimatsmuseum Neubrandenburg.

and the third valve mentioned by BOLL (*op. cit.*, p. 322) in a small tube, the outer part of which was crushed, but a small cotton-wool pellet deeply inserted in the tube had saved the specimens. Fragments of a label on the tube have the letters "*...ri...hia J...esi...*" and some ink points belonging to other letters. BOLL states that one specimen probably is "Lower Silurian" (= Ordovician) and the others "Upper Silurian" (= Silurian), but all are certainly Silurian in the present sense.

Beyrichia spinulosa BOLL 1856, a left tecnomorphic valve (Fig. 3 C), figured by BOLL (*op. cit.*) in his Fig. 3.

Beyrichia hians BOLL 1856, a left tecnomorphic valve (Fig. 3 D), figured by BOLL (*op. cit.*) in Fig. 4.

Next paper to be mentioned is also by BOLL (1862). Besides a series of identifications of earlier species he described the new species *B. Kochii*, *B. protuberans*, *B. cincta*, *B. spinigera*, and *B. elegans*; to *B. spinulosa* of 1856 he gave a new name (op. cit., p. 133). The following lectotypes, refigured here in Fig. 4, are designated here:

Beyrichia Kochii BOLL 1862, the right tecnomorphic valve (Fig. 4A) in BOLL's Pl. I, fig. 2.

Beyrichia cincta BOLL 1862, the left female valve (Fig. 4B) figured by BOLL in Pl. I, fig. 4.

Beyrichia elegans BOLL 1862, the fragmentary right female valve (Fig. 4C) in BOLL's Pl. I, fig. 10.

Other originals by BOLL are not of particular interest in connection with the present investigation.

BOLL made a subdivision of his *Beyrichia* species (which also included *Kloedenia wilckensiana*, with the subcruminal structures figured in Pl. I, fig. 14b) into four groups, *a*, *b*, *c*, and *d*, which he suggested should be elevated to generic rank in the future. He regarded the crumina as "a globularly swollen tubercle". Much space is devoted to the reconstruction of the stratigraphical and geographical origin of the erratics in the Palaeozoic of Sweden and in the Baltic countries.

The first Swedish paper on Silurian ostracodes was a thesis *pro gradu* by KOLMODIN 1869. He described three *Beyrichia* species, *B. lunata*, *B. clavata*, and *B. verrucosa*, from Gotland and a fourth species, *B. scanensis*, from Scania. The following originals in the Museum of the Institute of Palaeontology, Uppsala, are refigured in Figs. 5 and 6 and designated as lectotypes:

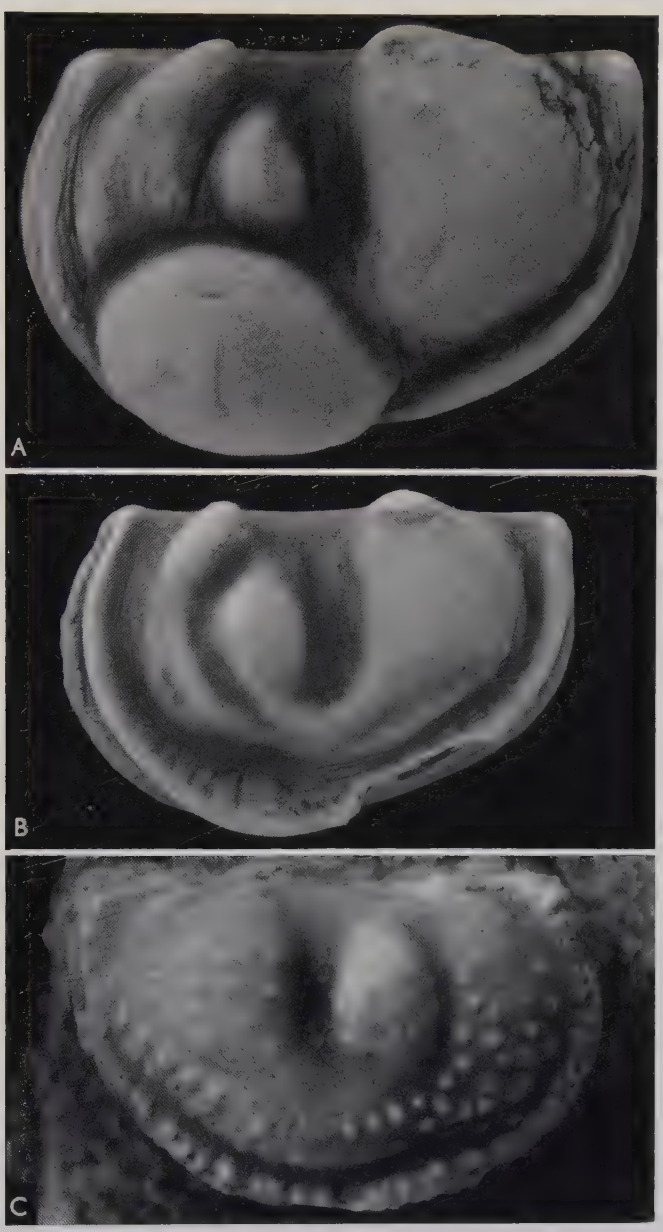
Beyrichia clavata KOLMODIN 1869, the left tecnomorphic specimen (Fig. 5B) in KOLMODIN's Fig. 10, from Djupvik, parish of Eksta, Gotland (Mulde Beds), designated as the lectotype by MARTINSSON (1956, p. 19; Pl. I, fig. 1, No. G 145), coll. N. P. ANGELIN (*fide* printed pink label stating: 14. *Battus Kloedeni*. Nob. Djupvik Gottlandiae. A-n).

Beyrichia lunata KOLMODIN 1869, the left female specimen (Fig. 5A) in KOLMODIN's Fig. 8, from Gotland (No. G 235), designated as the lectotype herein (only one label, similar to one of the labels in the tray of *B. clavata*). In the same tube was another specimen, probably identical with that figured by KOLMODIN as No. 9.

Beyrichia verrucosa KOLMODIN 1869, the right tecnomorphic valve (Fig. 5C) illustrated by KOLMODIN in Fig. 12, from Gannarve, parish of Fröjel, Gotland, together with several specimens on two pieces of calcareous shale (probably uppermost Slite Beds), designated as the lectotype herein (No. G 237), coll. P. T. CLEVE (*fide* label similar to that of *B. lunata*).

Beyrichia scanensis KOLMODIN 1869, the left tecnomorphic valve (Fig. 6C) in KOLMODIN's Fig. 11 (No. Sk 26). The specific identification admits of no doubt though the similarity between figure and original is minimal. KOLMODIN's label reads "Beyrichia Scanensis Skåne Ringsjön K.V.S. Saml." There are several specimens on 11 small limestone pieces. A female specimen among them is also figured here (No. Sk 27).

A further species referred to *Beyrichia* has been identified, viz. *B. bilobata*, represented by several external and internal moulds, It is a synonym of *B. costata* LINNARSSON (1869). KOLMODIN's thesis was defended on May 24th, 1869, and must have left the printer and been publicly nailed not later than a fortnight previously (the printers' firm, EDQUIST & BERGLUND, Uppsala, does not exist any more). Mr. S. VON PORAT, of P. A. NORSTEDT & SÖNER, AB, Royal Printers, states that during the first six months of 1869 the fascicles 9, 10, 1 and 2 of the "Öfversikt ..." series were printed and distributed; No. 2 with LINNARSSON's paper must have been printed very late during the six



No. G 235. Female carapace. × 30.

No. G 145. Tecnomorphic carapace. × 30.

No. G 237. Tecnomorphic right valve. × 30.

Fig. 5. KOLMODIN's originals illustrating new beyrichiid species from Gotland in 1869. A. *Craspedobolbina* (*Mitrobeyrichia*) *lunata* (KOLMODIN 1869), lectotype of *Beyrichia lunata* KOLMODIN 1869. B. *Craspedobolbina* (*Mitrobeyrichia*) *clavata* (KOLMODIN 1869), lectotype of *Beyrichia clavata* KOLMODIN 1869. C. *Beyrichia* (*Beyrichia*) *verrucosa* KOLMODIN 1869, lectotype of *Beyrichia verrucosa* KOLMODIN 1869. All in the museum of the Institute of Palaeontology Uppsala.

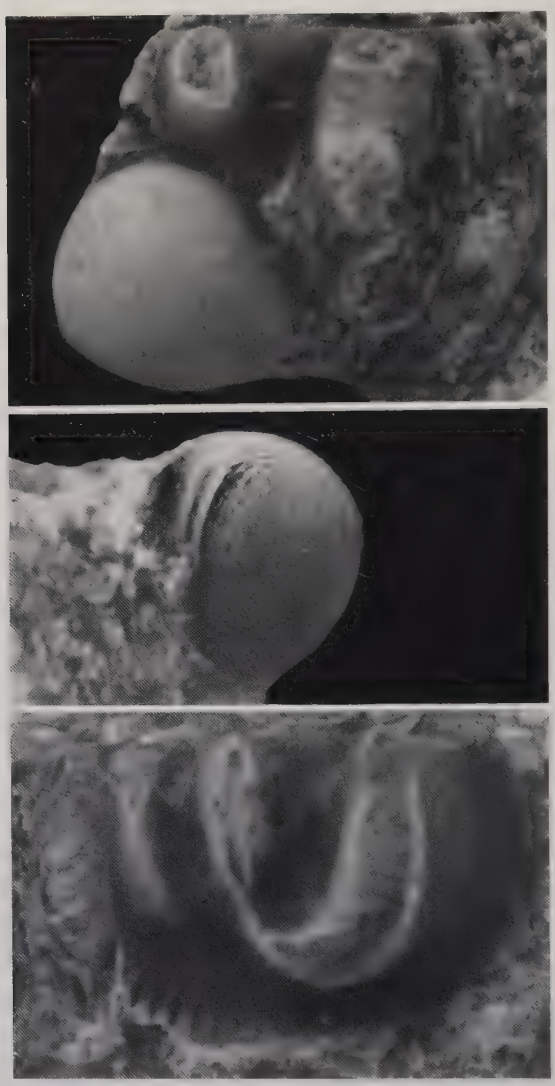


Fig. 6 A. *Lophoctenella scanensis* (KOLMODIN 1869), fragmentary left female valve from KOLMODIN's original material, No. Sk 26. × 40.

Fig. 6 B. Ventral side of the crumina of the same specimen. × 40.

Fig. 6 C. *Lophoctenella scanensis* (KOLMODIN 1869), lectotype of *Beyrichia scanensis* KOLMODIN 1869. × 40.

Fig. 6. Specimens from collections used by KOLMODIN 1869 for his description of *Beyrichia scanensis*, collected near Ringsjön in Scania. All in the museum of the Institute of Palaeontology, Uppsala.

months referred to. More exact information is not available. It is, then, probable that the important species *Steusloffia costata* (LINNARSSON) is a junior synonym of *B. bilobata*, a name which has not been recorded since the original description. Some of these facts and a review from the point of view of bassleratiid systematics have been given by JAANUSSON (1957, p. 373), and his proposal that KOLMODIN's specific name should be suppressed can only be supported.

In the same year RICHTER (1869, p. 774) discovered—or rediscovered—and first mentioned in print the cruminal dimorphism which will later be dealt

with extensively in this paper. He also recognized its sexual nature, and his statements are worth quoting in detail:

"Ebenfalls findet sich für die Randwulst der Beyrichien ein, wenn auch nicht vollkommenes, Analogon in der seitlichen Auftreibung des Panzers bei den weiblichen individuen von *Cythere gibba* Müll., so dass hiernach die Fossilien mit überquellender Randwulst als solche weiblichen Geschlechts betrachtet werden könnten. Es hat dies um so mehr für sich, als bei vielen ausgewachsenen Exemplaren diese Randwulst, welche bei den Individuen, die vermöge ihrer Kleinigkeit sich unverkennbar noch im Jugendzustande befinden, erst im Entstehen begriffen ist, statt überzuquellen, auffallend flach erscheint."

It is remarkable that the results of all recent discussions and elaborate investigations on the nature of the dimorphism and its appearance during the ontogeny have been established already in these few concentrated lines of 1869. This was the first kind of dimorphism in palaeocopes to be discovered.

In a second and final ostracode paper Kolmodin (1879) described *Beyrichia grandis* n.sp.

The original of Kolmodin's Pl. XIX, fig. 3 has been identified here as No. Ar 25645 in the collections of the Swedish State Museum of Natural History and is designated here as the lectotype (Fig. 7 A). As all edges in the specimen are missing and it has a coarse carapace structure, more like that of a trilobite, it looks more like a distorted *Calymene* fragment with a papillate lobe than an ostracode. However, a valve of a closely similar species was found in the lowermost Eke Beds of Lau backar. Very large quantities of marl have been surveyed in vain in order to find additional specimens. The two specimens in question are figured here (Fig. 7).

In 1885 Reuter extended the study of North German beyrichiids to East Prussia. The material described most probably does not contain any ostracodes as old as those from Gotland. The great variety of taxia with a dissolved syllobium constitutes a group which has been very little treated since then, and as far as we know there is no possibility of going back to Reuter's material to study it, as all his collections in Königsberg are believed to be lost.

Reuter's conception of taxionomy is somewhat extraordinary. He grouped most of his taxia into four developmental series, all of them derived from *B. tuberculata* in the classical sense. The extremities in these series were called species with binary names, and the taxia in between received an additional variety name.

Reuter founded these descriptions on an accurate terminology (op. cit., pp. 630–631) which would on the whole have suited modern needs if it had not been made impossible by the fact that Reuter orientated his ostracodes the wrong way. He discusses some older opinions about the function of the "swollen ventral lobe" and the situation of the sexual organs and concludes that they and, consequently, the crumina must be situated in the rear part of the carapace.

The continuation of this vivid discussion is in a paper by Jones & Holl from the following year (1886a). They discuss the problem complex involving

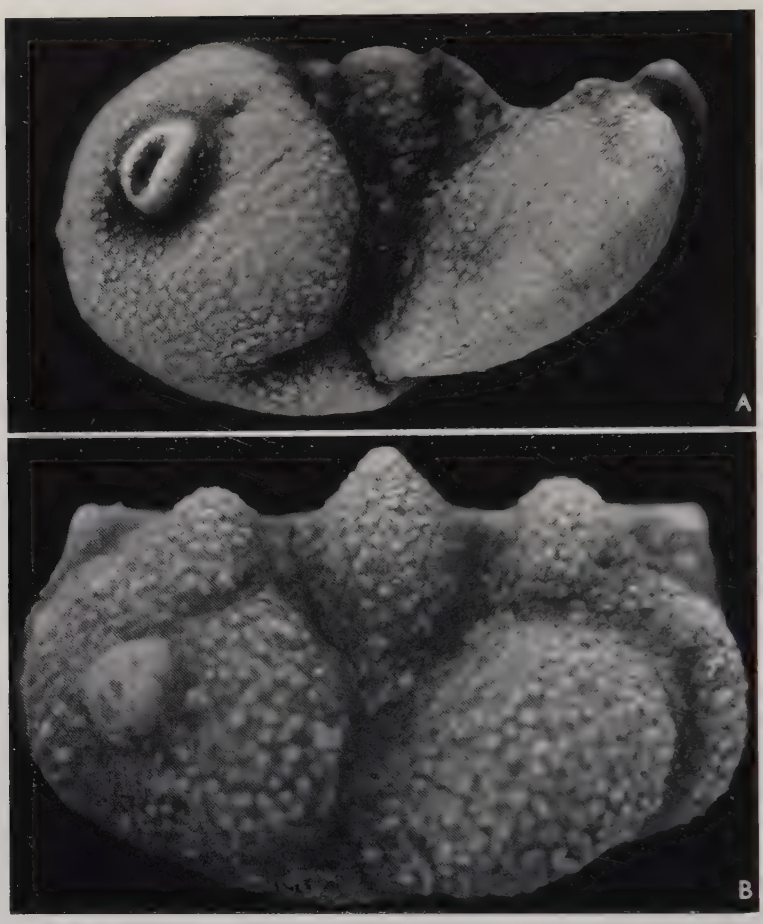


Fig 7. A. *Kolmodinia grandis* (KOLMODIN 1879), lectotype of *Beyrichia grandis* KOLMODIN 1879. RM No. Ar 25645. × 15. B. *Kolmodinia cf. grandis*, left valve from Lau Backar, No. G 239. × 30.

the function of the crumina, the orientation of the carapace and the correlation of dimorphs. They base their orientation on the fact that the postadductorial portion of the domiciliar part of the carapace space should be the more voluminous, in analogy with recent ostracodes, and propose two alternative interpretations of the crumina, viz. that they "might possibly have reference to a fully-developed hepatic gland" or that they "had a parasitic origin, like the swelling caused by *Bopyrus* in the Prawn". The beyrichiids in the SMITH and VINE collections are extensively treated, and the new genus *Kloedenia* is founded (op. cit., p. 362).

In another paper of the same year the same writers (JONES and HOLL 1886b) founded the genus *Strepula* and figured, without noticing it, the dimorphism in *S. concentrica*. A tecnomorph of a *Bolbiprimitia* species appears again under the name of *Primitia seminulum* (JONES 1855). These ostracodes also came from

the VINE and SMITH collections; as a complement to the taxionomical papers a list of the collecting localities, now largely spoiled, can be found in SMITH's paper of 1892.

The following lectotypes (cf. Fig. 2) are designated here:

Strepula concentrica JONES & HOLL, the complete tecnomorphic carapace (Fig. 2F) figured from the left side by JONES and HOLL (1886b) in Pl. XIII, fig. 6, from Woolhope (*fide* information on the label, also stating Smith's collection No. 55_3). According to JONES & HOLL, however, a left (= right with the orientation used by them) valve has been figured. As the distinction between "valve" and "carapace" is not always consistent in cases where only one side is figured, the label information has to be accepted. This is done, however, without full conviction that the type locality has been correctly given on the original label; the specimen was half buried in matrix of the Ironbridge type and has had to be prepared considerably before photographing. This specimen is No. IN 52531 in the collections of the British Museum (Nat. Hist.). JONES and HOLL figured two more specimens under this name, one of them an unidentified specimen (*op. cit.*, Pl. XIII, Fig. 4) of a beyrichiid from Lincoln Hill, Ironbridge, of the same kind as the other ostracodes referred to *Strepula*, and a small primitiopsid from the railway cut on the side of the Severn, Ironbridge, No. I 2392, Figs. 1a and 1b of the same plate. The only alternative to the selection of No. IN 52531 as the generolectotype of *Strepula* (*S. concentrica* was designated as the type species by BASSLER and KELLETT 1934) would be to chose No. I 2392 and make *Strepula* a primitiopsid genus. This would, however, make the complicated history of *Strepula* still more complicated.

Strepula irregularis JONES & HOLL, the right female valve (Fig. 2E) figured by JONES & HOLL (1886b) in Pl. XIII, fig. 7, from Lincoln Hill, Ironbridge, No. IN 52531. The male specimen in Figs. 8a and 8b of the same plate is No. IN 52909. *S. irregularis* is conspecific with *S. concentrica* as based on the lectotype designated above.

The next year JONES (1887) treated material from Gotland and recorded a new tecnomorph of a *Bolbiprimitia* as *Primitia seminulum*. The corresponding female was described as *Primitia inaequalis* n.sp., a *nomen nudum*. This is the second paper recording ostracodes from Gotland. In an appendix LINDSTRÖM listed the following beyrichids: *Beyrichia clavata* KOLMODIN, *B. Kloedeni* var. *granulata* JONES, *B. Kloedeni* var. *antiquata* JONES, *B. Kloedeni* var. *tuberculata* SALTER, *B. Bolliana umbonata* REUTER, *B. grandis* KOLMODIN, *P. seminulum* JONES, and *P. inaequalis* JONES. Other lists of ostracodes from Gotland, without further comments, were published by LINDSTRÖM in 1885 and 1888 (1888b).

JONES's studies on material from Gotland were continued the next year (1888a), when he figured the material, including a number of *nomina nuda*, from the preceding year. Large parts of this material have been identified in the Swedish State Museum of Natural History in a number of wooden slides with JONES's annotations on the back (cf. MARTINSSON 1956, p. 17). The material of *Primitia inaequalis* and *P. seminulum* has been figured earlier (MARTINSSON, op. cit., p. 24, Pl. V, figs. 50 and 51). Specimens of the other new species are refigured here in Fig. 11 and 12, and the following lectotypes are designated:

Kloedenia apiculata JONES 1888, the right female valve (Fig. 11A) in JONES's Pl. XXI, fig. 5, from Slite (No. Ar 25698:5). The other specimens figured in the same plate are:

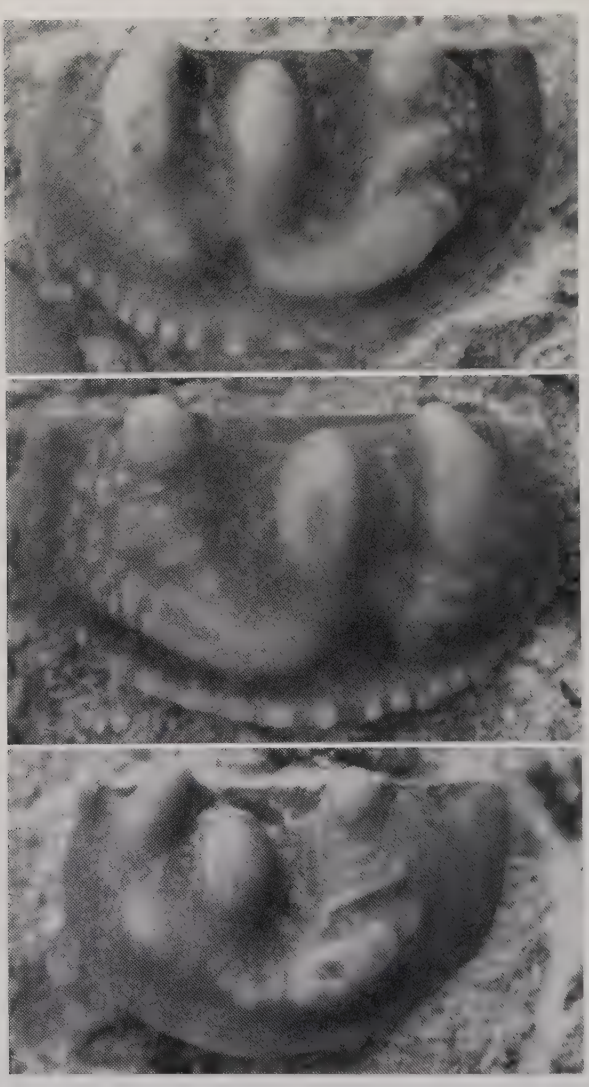


Fig. 8 A. *Beyrichia Lindströmi* var. *expansa* Kiesow 1888 (Pl. I, fig. 9). RM No. Ar 25684:2. × 30.

Fig. 8 B. *Beyrichia Lindströmi* var. *expansa* Kiesow 1888, lectotype. RM No. Ar 25684:1. × 30.

Fig. 8 C. *Beyrichia tuberculata* var. *Gotlandica* Kiesow 1888, lectotype. RM No Ar 25684:3. × 30.

Fig. 8. Specimens of *Neobeyrichia* (*Neobeyrichia*) *expansa* (Kiesow 1888) and *Calcaribeyrichia gotlandica* (Kiesow 1888) from a small slab, RM No. 25684, with Kiesow's original material.

Fig. 1 a–c, No. Ar 25698:2; Fig. 2, No. Ar 25698:6; Fig. 3, No. Ar 26598:3; Fig. 4, not identified; Fig. 5, No. Ar 25698:5.

Beyrichia tuberculata var. *spicata* Jones 1888, the fragmentary left female valve (Fig. 12 C) in Jones's Pl. XXI, fig. 13, from Slite (No. Ar 25893:3). Fig. 14 cannot be identified with certainty; the only remaining specimen which could be taken into consideration, No. Ar 25698:1, also a right female valve attached to a columnal disc of a crinoid, does not agree well with the figure which shows damage in the ventral part of the specimen.

Beyrichia tuberculata var. *foliosa* Jones 1888, the right female valve (Fig. 12 A) in Jones's Pl. XXI, fig. 17, from Slite (No. Ar 25893:2). Fig. 15 in the same plate is No.

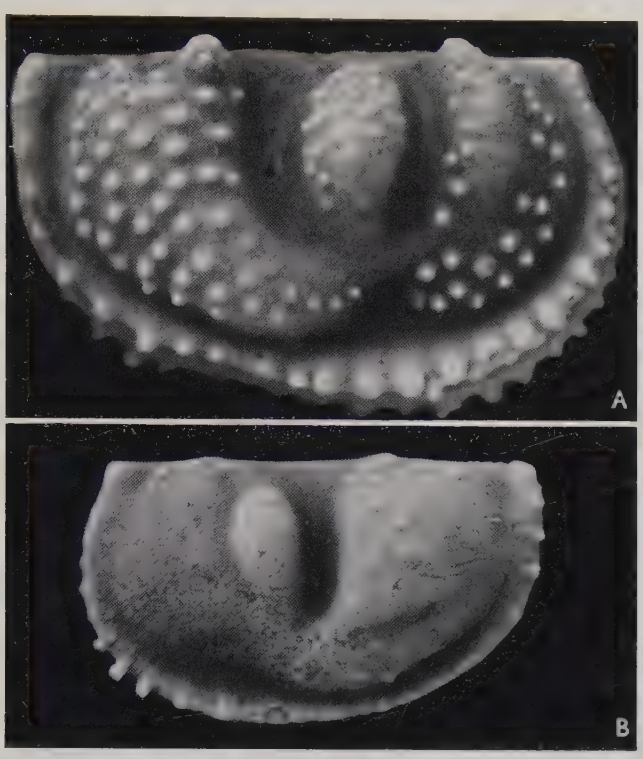


Fig. 9. A. *Neobeyrichia* (*Neobeyrichia*) *ctenophora* n.sp. B. *Beyrichia* (*Simplicibeyrichia*) *globifera* n.sp. Tecnomorphic carapaces. Originals of *Beyrichia Klödeni* var. *protuberans* BOLL by KIESOW (1888, Pl. II, figs. 4 and 5). RM Nos. Ar 25671 and 25674. × 30.

Ar 25893:1. The third specimen, Fig. 16, cannot be identified with certainty, probably it is identical with No. Ar 25893:5 which had disappeared from the slide before the rediscovery.

The other specimens figured in Pl. XXI are the following: *Beyrichia clavata* KOLMODIN: Fig. 6, probably No. Ar 25644:1; Fig. 7, No. Ar 25644:2; Figs. 7–9 cannot be identified. *B. bolliana-umbonata* REUTER (tecnomorphs of *B. subornata* MARTINSSON): Fig. 10, No. Ar 25697: 8: 1; Fig. 11, No. Ar 25697: 8: 2. The remaining beyrichiids, in Pl. XXII, viz. *Primitia seminulum* (JONES) and *P. inaequalis* JONES, have the numbers Ar 25697: 1 and Ar 25697: 3, respectively. They were revised as *Bolbiprimitia inaequalis* (JONES), with the designation of a lectotype, by MARTINSSON (1956, p. 24; Pl. V, figs. 50 and 51).

JONES's figures of the spinose "varieties" represent matrix parts almost as much as ostracodes, and it would have been very difficult to identify most of them if they had not been investigated and figured before further preparation. They are mounted on the bottoms of seven slides of cedar wood, Nos. Ar 25644, 25656, 25697, 25698, 25726, 25727, and 25893. They have been closed by label paper but reopened later on. The specimens within the numbers quoted have been numbered with a pencil, but between that and the rediscovery several specimens had disappeared.

In another paper of the same year JONES (1888b) introduced the new Devonian beyrichiid genus *Kyamodes*.

Fig. 10. *Neobeyrichia* (*Neobeyrichia*) *lauensis* (Kiesow 1888). A. Specimen from Burs, near the type locality, in Krause's collections in Berlin. Collector unknown; the probability is in favour of Kiesow. ×20. B. Neotype, designated herein, from Botvide in Lau, No. G 621. ×20.

The papers by Jones have been treated here as a series, for the sake of convenience. Already before those of 1888 Kiesow had published a paper on beyrichiids from Gotland (1888), discussing the orientation starting from the premise that "*Beyrichia*" *oculifera* Hall had facetted eyes anteriorly. He also states, basing his discussion on analogies with *Cythere gibba* Müller like the previous writers on the same problem, that the cruminae were used for brood care. Most of his figures are very good for their time, and, as mentioned above, his new figures of *Beyrichia Jonesii* Boll are of essential importance for the identification of the type material. The originals of his new taxia, except for *B. Lauensis*, *B. Lindströmi*, and *B. Buchiana* var. *nutans* (cf. p. 321) have been identified in the State Museum of Natural History, Stockholm. The others belong to Kiesow's own collections; the depository is not known, but it has been established that they are not included in the collections in Berlin. The following lectotypes (cf. Figs. 8, 9, and 11) are designated here:

Beyrichia tuberculata var. *Gotlandica* KIESOW 1888, the left tecnomorphic valve (Fig. 8C) in KIESOW's Pl. I, fig. 1, the only specimen known, No. Ar 25684: 3, from the lower part of the Hemse Beds of Östergarn, Gotland.

Beyrichia Lindströmi var. *expansa* KIESOW 1888, the right tecnomorphic valve (Fig. 8B) in KIESOW's Pl. I, fig. 8 (No. Ar 25684: 1), from the lower part of the Hemse Beds of Östergarn, Gotland. Fig. 9 in the same plate is No. Ar 25684: 2. Fig. 7, which is not drawn with G. LILJEVALL's naturalistic skill like the others, is probably a fourth specimen on the small slab No. Ar 25684.

Beyrichia Klödeni var. *bicuspis* KIESOW 1888, the left tecnomorphic valve (Fig. 11F) in KIESOW's Pl. II, fig. 6, from the uppermost Slite Beds at Kvarnberget (Quarnberget), Slite, Gotland (No. Ar 25679: 1). Fig. 7 in the same plate is No. Ar 25679: 2.

Unfortunately the originals of the important new species *Beyrichia Lauensis* (cf. KIESOW 1888, Pl. II, figs. 1–2) cannot be traced. Some ostracodes collected by KIESOW seem to have been included in KRAUSE's collections in Berlin. In these collections there are also specimens of *B. Lauensis* (Fig. 10), constituting the only contemporaneous collections of the species identified. As they are labelled "Burs", a parish adjoining that indicated as the type locality (Lau) it cannot be used as a type. Material is obtainable from Lau, and a neotype is designated on p. 318. KIESOW's originals of *B. Klödeni* var. *protuberans* BOLL have also been identified, cf. Fig. 9.

ULRICH (1891) described the new species *Beyrichia lyoni* in his first ostracode paper. It is the type species of the new genus *Treposella* ULRICH & BASSLER 1908.

CHAPMAN (1901) published a study on ostracodes from the Mulde Beds of Gotland to which JONES added a systematic table of the ostracode genera known from Gotland. He described three new "beyrichiids":

Kloedenia gotlandica CHAPMAN is not a beyrichiid. *Beyrichia muldensis* CHAPMAN is an ulrichiid according to present concepts of that family. *Beyrichia Kloedeni* var. *lineato-tuberculata* CHAPMAN is a fragmentary right tecnomorphic valve of a *Beyrichia* (*Beyrichia*) species almost completely concealed by a marl cover. On the evidence of hundreds of thousands of beyrichiids in the Mulde fauna there are only three spinose *Beyrichia* species which can be identical with this "variety". The specimen deposited in the British Museum (Nat. Hist.) as CHAPMAN's original (No. I 3775) is not identical with the figure. It is a clean complete female carapace of *Beyrichia peponulifera* described below. The label says "Purch. M. DANCET, Nov. 1900"; the specimen described was from another collection given to CHAPMAN "some few years" earlier by F. R. BATHER. *B. Kloedeni* var. *lineato-tuberculata* is, under these circumstances, clearly a *nomen dubium*.

T. R. JONES's conceptions of the systematic position of the beyrichiids found on Gotland were, according to the table in CHAPMAN's paper the following:

Family *Leperditiidae* JONES
  Subfamily *Aparchitinae* n.subf.
    Primitia JONES & HOLL 1865
  Subfamily *Beyrichiinae* n.subf.
    Kloedenia JONES & HOLL 1886
    Beyrichia M'COY 1846

In this connection the early conceptions of the family should be reviewed. In 1886 MATTHEW had distinguished the subfamily *Beyrichinae* (original

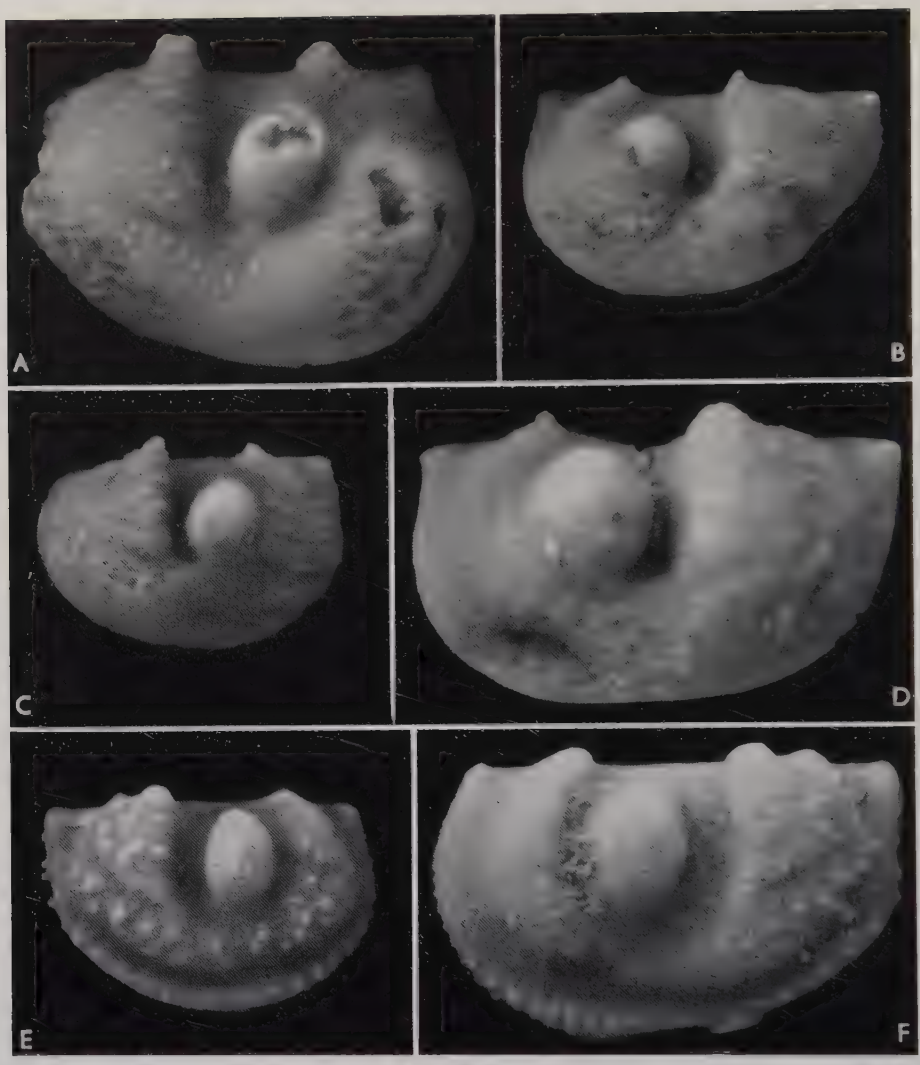


Fig. 11. Originals of ostracodes figured by Kiesow 1888 and Jones 1888 a. A–D. *Beyrichia* (*Asperibeyrichia*) *apiculata* (Jones 1888), all specimens figured by Jones 1888 a, Pl. XXI (cf. p. 25). A. Lectotype of *Kloedenia apiculata* Jones 1888, right female valve, RM No. Ar 25698:8. × 30. B. Left tecnomorphic valve, RM No. Ar 25698:6. × 30. C. Right tecnomorphic valve, RM No. Ar 25698:2. × 30. D. Left tecnomorphic (male) valve, RM No. Ar 25698:3. × 30. E. *Beyrichia* (*Beyrichia*) *hellviensis* n.sp., right tecnomorphic valve, figured by Kiesow 1888, Pl. II, fig. 7 as *Beyrichia Klödeni* var. *bicuspis*. RM No. Ar 25679:2. × 30. F. *Beyrichia* (*Beyrichia*) *bicuspis* (Kiesow 1888), lectotype of *Beyrichia Klödeni* var. *bicuspis* Kiesow 1888. RM No. Ar 25679:1. × 30. The specimen is figured before the removal of the matrix for documentary reasons; it shows the characteristic matrix piece below the velum also seen in Kiesow's figure (1888, Pl. II, fig. 6).

spelling) to include a number of beyrichiids and new Middle Cambrian problematic ostracodes described by him.

The subsequent work on finding the systematic position and limitation of the *Beyrichiidae* is largely characterized by the gradual expulsion of the in-

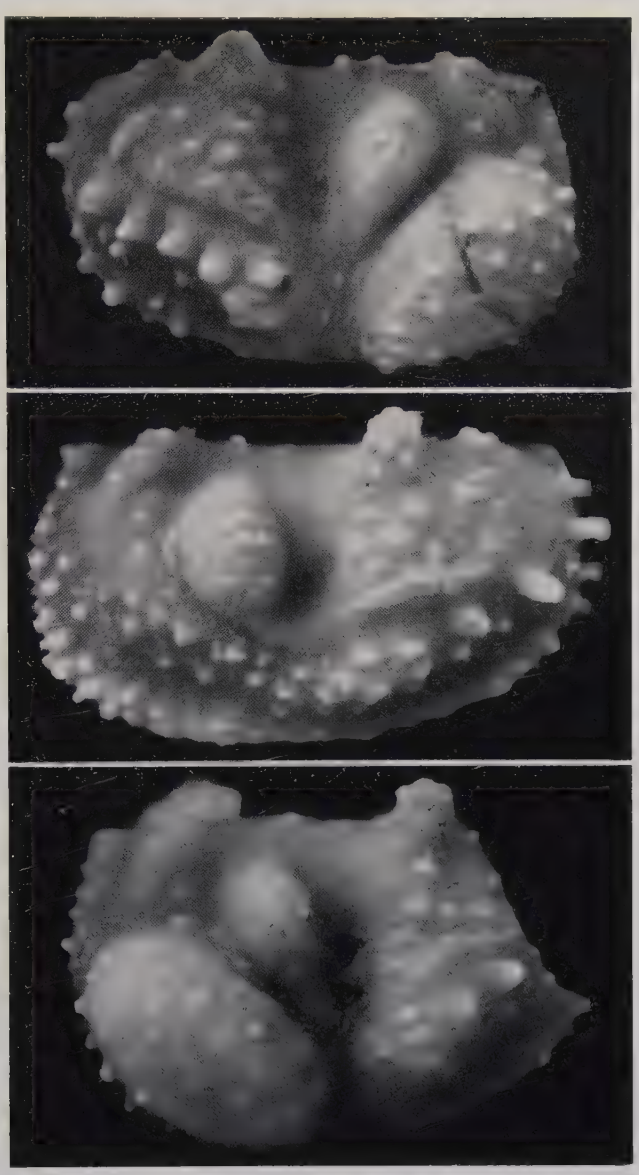


Fig. 12 A. Right female valve. RM No. Ar 25893:2. ×30.

Fig. 12 B. Left male valve. RM No. Ar 25893:1. ×30.

Fig. 12 C. Left female valve. RM No. Ar 25893:2. ×30.

Fig. 12. Originals figured by JONES 1888 a. A. *Beyrichia* (*Scabribeyrichia*) *foliosa* (JONES 1888) lectotype of *Beyrichia tuberculata* var. *spicata* JONES 1888. B. Same species, original of JONES 1888 a, Pl. XXI, fig. 15. C. Same species, lectotype of *Beyrichia tuberculata* var. *spicata* JONES 1888. The striking differences in morphology in comparison with the original illustrations is explained by the fact that these illustrations include much matrix substance.

creasing number of genera referred to this "leading family" among fossil Palaeozoic ostracodes. In 1908 ULRICH and BASSLER stated: "As defined in modern text-books, the Paleozoic family of Ostracoda, Beyrichiidae, embraces a large and constantly growing assemblage of genera and species." At least

one of these text-books, viz. that by MILLER (1889, p. 523) is older than ULRICH's systematic survey of 1897 (preprinted 1894) which is often regarded as the designation reference of the family name *Beyrichiidae* (the concept of family group names did not exist then).

In his "Provisional classification of the Paleozoic Ostracoda" ULRICH (op. cit.) referred 22 genera to the family *Beyrichiidae*; only three of them are beyrichiids in the present sense, viz. *Beyrichia*, *Kloedenia*, and *Strepula*. The genus *Kyamodes* was referred to the family *Barychilinidae* together with the type genus of this family.

Mainly the same system, containing most of the suborder *Palaeocopa* in the present sense, appeared in ULRICH and BASSLER's revision of the family (1908). They also discuss the orientation of the carapaces, referring to the thinning out forwards of the carapace (in lateral view; earlier writers, who paid more respect to the distribution of the domicilial space than to the outline must have seen their specimens in dorsal view, which leads to the opposite conclusion), the retral (by the other school called "forward") swing of the outline, the earlier misinterpretations of "*Beyrichia*" *clavigera*, and to the position of the brood pouches. This reverse orientation has left many traces in later literature. The genus *Treposella* was introduced in this paper (p. 314).

In a paper of 1916 ULRICH added the new genus *Zygobeyrichia* from the Devonian of Maine.

In 1923 ULRICH and BASSLER introduced the superfamily *Beyrichiacea* (p. 297), roughly covering all palaeocope ostracodes. In this first extensive systematic revision of the palaeozoic straight-hinged ostracodes the family *Beyrichiidae* was considerably restricted, and the genera now known to be cruminate were placed in the superfamily as follows:

Superfamily *Beyrichiacea* n.superf.
- Family *Primitiidae* n.f.
  - Subfamily *Primitiinae* n.subf.
    - *Bolbibollia* n.g.
  - Subfamily *Eurychilininae* n.subf.
    - *Apatobolbina* n.g.
- Family *Zygobolbidae* n.f.
  - Subfamily *Zygobolbinae* n.subf.
    - *Zygobolba* n.g.
    - *Zygobolbina* n.g.
    - *Zygosella* n.g.
    - *Bonnemaia* n.g.
  - Subfamily *Kloedeninae* n.subf.
    - *Plethobolbina* n.g.
    - *Mastigobolbina* n.g.
    - *Kloedenia* JONES & HOLL
    - *Welleria* n.g.
    - *Kyamodes* JONES
    - *Zygobeyrichia* ULRICH

Subfamily *Drepanellinae* n.subf.
Drepanellina n.g.
Mesomphalus n.g.
Family *Beyrichiidae* JONES (restricted)
Beyrichia M'COY
Dibolbina n.g.
Treposella ULRICH & BASSLER
Family *Kirkbyidae*
Strepula JONES & HOLL

ULRICH and BASSLER's criteria in classifying fossil ostracodes are found in the paper quoted on pp. 285–287. Among the generic characters lobation is attributed primary importance which explains much of the above system. However, in the *Beyrichiacea* respect was also paid to sex characters, though the distinction between dolonal and cruminal pouches had not been made yet.

KUMMEROW (1924) published the first records of *Apatobolbina* from Europe and figured two treposelline species, *Beyrichia acutiloba* n.sp. and *Halliella umbonata* n.sp. A fourth species in the same genus as the previously described *Beyrichia jonesi*, *B. clavata*, and *B. lunata* was described as *Craspedobolbina dietrichi* n.g., n.sp.

KUMMEROW's originals of *Craspedobolbina dietrichi* have not been identified, but there are additional specimens in KUMMEROW's collections in the collections of the Palaeontological Museum of the HUMBOLDT University in Berlin, and there is no doubt that they are conspecific with the ostracodes figured by KUMMEROW (op. cit.) in Pl. 20 (incorrectly numbered 21), figs. 27 and 28. They confirm the immediate impression that the figures represent a tecnomorphic and a female specimen, the velum and anterior cardinal corner of which are broken away, of a species belonging to the same genus as *B. jonesi* BOLL, the type species of *Mitrobeyrichia* HENNINGSMOEN 1954, here conserved as a subgenus of *Craspedobolbina*. The species is probably Llandoverian or early Wenlockian in age; all known *Craspedobolbina* species in the bedrock of the Baltic area with the same zygal and syllobial morphology are of this age. *Craspedobolbina* has been associated with a quite different group of beyrichiids by HENNINGSMOEN (1954). HENNINGSMOEN (1954, p. 63, and 1955, pp. 241 and 245) had some doubt as to KUMMEROW's interpretation of the age of the species but regarded it, followed by KESLING (1957, p. 63), as the oldest known beyrichiid. Even if the age is disregarded, however, it is one of the most primitive ones, as shown by congeneric species described here.

The following lectotype is designated here (cf. Fig. 13A).

Craspedobolbina dietrichi KUMMEROW 1924, a right, probably young, tecnomorphic valve in limestone matrix, attached to the cork of a small glass tube in KUMMEROW's collection. This is at present in the Palaeontological Museum of the HUMBOLDT University in Berlin (cf. DIEBEL 1960) after having been handed back to the Berlin Museums by the U.S.S.R. In the tube were four other valves on rock fragments. These are the only

Fig. 13. *Craspedobolbina* (*Craspedobolbina*) *dietrichi* KUMMEROW 1924. Small tecnomorphs constituting the larger part of the autohyle material of *Craspedobolbina dietrichi* KUMMEROW 1924. Fig. 13 A is the lectotype of this species. × 50.

specimens of the species known. A label in the tube, in KUMMEROW's handwriting, has the text: "Craspedobolbina Dietrichi Km. Hoh. Ferchesar.".

STRAW's revision of the type species of *Beyrichia* appeared in 1928. Another British reference of interest is HARPER's (1940) paper on Upper Llandoverian beyrichiids. For the rest, the European discussion touching beyrichiid questions 1924–1941 was dominated by a printed correspondence on brood care and orientation between KUMMEROW, who had adopted his orientation norms from ULRICH and BASSLER, and BONNEMA who, after a lucid and excellently illustrated study on Ordovician palaeocopes (1909), had adopted the opposite opinion. This discussion can be followed backwards through the references in BONNEMA's last paper in the series (1938). After TRIEBEL's study on these questions (1941) ULRICH's and BASSLER's orientation was generally abandoned, as far as beyrichiaceans are concerned, even by KUMMEROW (1948, except Fig. 4); the only writer to maintain it later is SPJELDNAES (1951, except Pl. 103, fig. 7).

BASSLER and KELLETT (1934) largely repeated the classification proposed by ULRICH and BASSLER (1923).

SWARTZ (1936) continued the restriction of the *Beyrichiidae* which he placed together with the *Zygobolbidae* in a special division of the *Beyrichiacea*, suggesting that this and three other divisions should be regarded as superfamilies if their limitation was supported by further studies. His family *Beyrichiidae* contains six cruminate genera, *Apatobolbina*, *Bolbibollia*, *Craspedobolbina*, *Beyrichia*, *Dibolbina*, and *Treposella* together with four genera with dolonal dimorphism, *Coelochilina*, *Apatochilina*, *Eurychilina*, and *Chilobolbina*.

SWARTZ founded his system in a considerable degree on differences in the dimorphic characters, but he did not find the distinction between cruminal and dolonal pouches.

This distinction represents the next advance of beyrichiid systematics. ULRICH and BASSLER (1923, p. 278) had demonstrated that some "brood pouches", as in *Beyrichia* and the *Zygobolbidae*, opened inside the contact edges of the valves, but others, as *Primitiopsis*, had the opening of the pouch outside them; *Chilobolbina* was regarded as a transition between them, but it could not be established how its pouch opens. ÖPIK (1937) and THORSLUND (1940) settled this by demonstrating in different ways that it opens outside the edges. HESSLAND (1949, pp. 123–128) distinguished between three types of dimorphism, two of which, the *Eurychilina* and the *Chilobolbina* types, are characterized by "swellings of the vela", and the third, the *Beyrichia* type, by "swellings of the carapace wall".

The function of the crumina was discussed again by TRIEBEL (1941, pp. 362–365) who believed that the crumina could be a consequence of the complicated sexual apparatus of male ostracodes. HESSLAND, however, found small specimens in the carapace of a cruminate beyrichiid the carapace of which had certainly not been opened after death (1949, Pl. XV, fig. 9) and concluded that they must be larvae. SPJELDNAES (1951) proved that the cruminae very often contain brood. The same study was repeated with the same results by MARTINSSON (1956, p. 14) who also checked a large number of closed male carapaces without finding any larval specimens in them. All these studies were carried out on thin sections of *Craspedobolbina clavata* (KOLMODIN), though its name varies (*Beyrichia kloedeni* M'COY in HESSLAND, op. cit., *B. jonesi* BOLL in SPJELDNAES, op. cit., and *B.* (*Mitrobeyrichia*) *clavata* (KOLMODIN) in MARTINSSON, op. cit.).

SCHMIDT (1941) introduced the term *velum* for the pouch-forming adventral structure.

SPJELDNAES's paper (1951) contains a large number of new details and ideas, all based on observations of the very well-preserved population (ecodeme), of *Craspedobolbina clavata* (determined as *Beyrichia jonesi*, cf. above) from Mulde on Gotland. He described the internal structures of the pores of the carapace wall and the tubulous structure of the velum and the marginal structure. He identified, however, SCHMIDT's "Schliessaum" (1941, Fig. 1a) with the "velum" and picked up the term "carina" for the "velum" *sensu* SCHMIDT.

His opinion on the ontogeny of these structures is very difficult to understand: "The velum seems to have been gradually reduced during ontogenetic development and replaced by the carina, which is probably homologous." The marginal structure (velum *sensu* SPJELDNAES) and the velum (carina *sensu* SPJELDNAES) are definitely two different structures, in well-preserved specimens of all stages always present together, and cannot be homologous. He also observed the posterior larval acroidal process which, as he used the reverse orientation of the valves, was interpreted as a rostrum, one of the several arguments used for illustrating the relationships of *Beyrichia* with the *Myodocopa*. According to SPJELDNAES, furthermore, the larvae moulted once or twice before leaving the crumina, and there are nine free stages. The possibilities of preadult dimorphism are also discussed (op. cit., p. 751) but the material referred to has later proved to belong to two different species.

The next step forward in beyrichiacean systematics with respect to the typical family itself was HENNINGSMOEN's series of revisions (1953, 1954, and 1955; intervening papers dealing with larger parts of the beyrichiacean system, by KAY 1940, SCHMIDT 1941, and HESSLAND 1949, have no direct bearings on this paper, except for the erection of *Bolbiprimitia* KAY). He separated the straight-hinged palaeozoic ostracodes in a special suborder, *Palaeocopa* (1953), and arranged his system more firmly after dimorphic and other adventral characteristics than had been the case before. His family *Beyrichiidae* is based on the existence of the cruminae. The large genus *Beyrichia* was divided into subgenera (unfortunately the type species of these were either lost during the war, known only as one dimorph, preserved only as moulds, incompletely known only from erratics, or combinations of these factors; in *B. kloedeni* this was, of course, unavoidable). In his system cruminate ostracodes appear in the following way (1955, 1953):

Order *Ostracoda* LATREILLE 1802
  Suborder *Palaeocopa* HENNINGSMOEN 1953 (original spelling *Paleocopa*)
    Family *Beyrichiidae* JONES 1894
      Subfamily *Beyrichiinae* JONES 1894
        Beyrichia (*Beyrichia*) M'COY 1846
        Beyrichia (*Eobeyrichia*) HENNINGSMOEN 1954
        Beyrichia (*Mitrobeyrichia*) HENNINGSMOEN 1954
        Beyrichia (*Neobeyrichia*) HENNINGSMOEN 1954
        Beyrichia (*Nodibeyrichia*) HENNINGSMOEN 1954
        Beyrichia (*Velibeyrichia*) HENNINGSMOEN 1954
        Craspedobolbina KUMMEROW 1924
        Apatobolbina ULRICH & BASSLER 1923
        Bolbibollia ULRICH & BASSLER 1923
        Dibolbina ULRICH & BASSLER 1923
      Subfamily *Zygobolbinae* ULRICH & BASSLER 1923
        Bonnemaia ULRICH & BASSLER 1923
        Mastigobolbina ULRICH & BASSLER 1923
        Plethobolbina ULRICH & BASSLER 1823

Zygobolba Ulrich & Bassler 1923
Zygobolbina Ulrich & Bassler 1923
Zygosella Ulrich & Bassler 1923
Subfamily *Kloedeniinae* Ulrich & Bassler 1923
Cornikloedenia Henningsmoen 1954
Drepanellina Ulrich & Bassler 1923
Kloedenia Jones & Holl 1886
Kyamodes Jones 1888
Welleria Ulrich & Bassler 1923
Zygobeyrichia Ulrich & Bassler 1923
Subfamily *Treposellinae* Henningsmoen 1954
Bolbiprimitia Kay 1940
Hibbardia Kesling 1953
Mesomphalus Ulrich & Bassler 1923
Phlyctiscapha Kesling 1953
Treposella Ulrich & Bassler 1913

The only genus included in Henningsmoen's system which he did not know to be cruminate, is *Strepula*, which is found in the family *Tetradellidae* (*Bassleratiinae*). Pokorný (1958) adopted this system entirely, except that he, referring to the similarity between *Beyrichia* and *Kloedenia* (certainly *sensu* Ulrich & Bassler, not *sensu* Jones), merged the subfamilies *Beyrichiinae* and *Kloedeniinae*.

In Jaanusson's important revision of the palaeocope system (1957) a clear distinction of the cruminate dimorphism was made, and the groups not having this dimorphism were broken out as separate superfamilies. Family-group names outside the *Beyrichiacea* quoted below follow the system as outlined by Jaanusson (op. cit., p. 222), with the addition of *Primitiopsacea*.

This survey has had as one of its objects to release the main parts of the present paper from a heavy but necessary survey of the historical background. The development during the last ten years has resulted in several important publications and in parts of the last-mentioned papers which are so engaged in the current discussion that it would be an unnecessary repetition to review them in detail here. With reference to the discussion below and the literature quoted later on, only the following summary of general trends in the beyrichiacean (*s.str.*) investigations will be given.

New important Silurian faunas have been described mainly from Norway (Henningsmoen 1954), Siberia (Abušik 1960), New Jersey and New York (Swartz and Whitmore 1956), and Nova Scotia (Copeland 1960). New taxia from America have been described by Kesling and collaborators to wh m we owe the main part of our knowledge of Devonian forms. The first occurrence of *Beyrichia* (*Beyrichia*) in America was recorded by Martinsson (1960c).

Much attention has been paid to the ontogeny of beyrichiids and related palaeocopes, especially by Adamczak in Poland, Kesling and collaborators in the U.S.A., and Martinsson in Sweden. Martinsson has particularly investigated the nature of the cruminal dimorphism and its appearance during

the ontogeny. HENNINGSMOEN and KESLING (KESLING 1957b) in particular have presented modern ideas on the phylogeny of the beyrichiids.

The accuracy of descriptions and figures has increased considerably. The palaeocope terminology has been defined more strictly by KESLING, HENNINGSMOEN, JAANUSSON and MARTINSSON; KESLING's paper of 1951 is the key to the understanding of terms used by earlier authors or in different languages. Several important beyrichiids have been refigured in detail, most of them collected in the paper by KESLING and RODGERS (1957), but real type revisions are still comparatively few.

Morphological details, except for lobation and adventral structures, have been studied especially by ADAMCZAK and by POKORNÝ, who has devoted extensive studies to the hinge and its systematic relationships. The adventral structures are more or less extensively treated in all modern beyrichiid papers, and the most thorough analysis of the systematic importance of these structures in the palaeocopes and of the dimorphism associated with them has been made by JAANUSSON (1957).

Further references and reviews of beyrichiid genera not mentioned above will be given in the respective sections below.

Methods

The literature on the collecting and preparation of microfossils is extensive and steadily increasing. The reader is referred to the excellent summary by POKORNÝ (1958, Vol. I, pp. 5–24) which also contains an extensive bibliography (*ibidem*, pp. 470–475). However, much of the preparation technique described hitherto has been worked out on Mesozoic and Tertiary rocks and fossils, and many of the methods cannot be used or are even injurious when working with Early Palaeozoic material. It is, therefore, justifiable to describe those methods, some of them new or modified, which have been found most applicable on material of the kind treated here and to give some insight into the nature of the material by shortly describing the sampling conditions.

COLLECTING.—Experience from earlier investigations of a similar kind shows that it is particularly desirable to obtain an abundant material which is sufficiently well-preserved and preparable to make possible an investigation even of the details in the delicate adventral structures. Therefore, the investigation has been concentrated to material from the marly facies. The risk of missing important faunal elements from the more calcareous facies by this method has already been discussed (p. 12); on the other hand it is an advantage to follow the development within a fairly uniform facies.

The rocks traditionally called "marls" or "marlstones" on Gotland are argillaceous rocks with a content of calcium carbonate of 10–80% (cf. HEDE 1925a, p. 8). They have never been investigated in detail petrographically.

The argillaceous components are dominated by the clay fraction in the strict sense, and the rocks are, then, finer grained than most rocks termed "marls" or "calcareous shales" farther west in Europe. The unweathered marly rocks have a very different degree of consolidation. The percentage of calcium carbonate does not seem to be a good exponent of the degree of consolidation, as some of the marls with abundant fossil fragments seem to contain very little calcareous matter between these fragments, and *vice versa*. The marly rocks form rock units which can be almost homogeneous through several tens of meters; in other cases they are interbedded with limestone strata of varying thickness. Many samples also come from occasional thin intercalations of varying horizontal extension in thick limestone sequences or from marly lenticles or irregular "marl pockets" in the reefs and on the flanks of the reefs.

With few exceptions the rock has had to be considerably weathered before a sufficient ostracode material can be obtained, which explains why so little of the material described comes from quarries worked in recent times. Most of the best localities are in old ditches, in the raised cliffs (clints), other shore exposures, and in abandoned quarries. The material has generally had to weather some tens of years before the ostracodes can be washed out with ease. The fossils themselves have very seldom (except in the Tofta Beds) been affected by weathering in the localities chosen.

The size of the samples from each locality as indicated below varies from about 2 to 200 kilograms (from Mulde more than twice this weight); most of the localities are represented with about 10 kg. They are generally concentrated to some decimeters of the sequence, sometimes to a few meters. When possible the samples have been subdivided into small portions within the sections at the respective localities, but only in one or two cases (see the list of localities below) is there a possibility that material from two different biostratigraphic units could have been mixed.

The composition of an ostracode sample from one of the best localities has been described earlier (Martinsson 1956, p. 5), with about 12.000 specimens in a 115 cm^3 bag of unconcentrated marl. Several other samples contain only one or two specimens in the same quantity, and even in the largest samples there are species which could not be treated as they are known only as a single tecnomorphic valve.

Washing and Extraction of the Material.—The marl samples have been disintegrated in hot water, washed, and fractioned through screens with 2, 1, 0.5, 0.25, 0.125, and, for some samples, 0.006 mm meshes. Chemical-physical disintegration methods have been applied with less success, as they tend to break the carapaces into pieces rather than to break away the matrix. The fractioning of the washing residue has proved to save a great deal of time during the extraction.

The extraction has been made on black trays ruled into squares of convenient size for the different sets of objectives and oculars used. To pick material of

this kind the "wet method", as earlier described (Martinsson 1956, p. 4), has been found most convenient, implying that the ostracodes are picked with an alcohol-moistened brush and are detached from it by dipping the brush into a embryo dish filled with alcohol. Owing to the rapid evaporation of the alcohol contaminations consisting of fossil or matrix fragments can easily be removed from the brush. Water has too great a surface tension and evaporates too slowly to be used for rapid extraction work. Material picked with wax on needles or glycerine on brushes must be subjected to special cleaning procedures before being covered with ammonium chloride for photographing.

Selective Extraction.—A very large material is needed for certain purposes, such as obtaining female ostracodes with incomplete cruminal metamorphosis or adult specimens of very rare species. For this purpose the extraction of hundreds of kilograms of material has been concentrated only to the convenient size fraction which has, in some instances, been still more restricted by putting additional screens between those with the mesh sizes mentioned above. The spinose *Beyrichia* species from Mulde, e.g., could not have been distinguished from each other without this method.

Individual Preparation.—As mentioned above the chemical-physical methods of breaking away the matrix from the fossils mostly damage these forms considerably. Small, isolated fragments of matrix are not broken away. The ornamentation of the finely reticulate forms is broken away almost entirely, as the formation of gas bubbles or crystals takes place even in the small puncta or meshes in the reticular pattern. Therefore, all specimens figured or studied in any detail have been cleaned by the following method.

The bottom of an embryo dish is covered with a thin film of a cement of cellulose acetate type (the Swedish brand Karlsons Klister, exported under the name "KK 33" and made by Klärre & Co., A.B., Box 9119, Stockholm 9, has proved to be excellent for this purpose). If the film shows a tendency to loosen from the glass surface, the adhesive property of the glue can be considerably improved by smearing a drop of it against the bottom of the dish with a finger until it becomes very tough. A small drop of the same cement is placed on the film and is spread on it in a layer of convenient thickness. The fossil is very rapidly placed in the fresh cement and orientated. If necessary, especially if a valve has to be placed on edge, the cement can, during the next ten seconds or so, be drawn out into narrow strips which can be placed across the fossil and be attached at the other side; this attachment must often be made by means of a fine brush moistened in acetone.

During the latter part of the work the manufacturer of KK 33 has kindly provided a special cement the solvent of which makes it especially useful for this method.

The cement is left to harden. Often the preparation can begin already after some minutes, but if firmly attached matrix or fossil fragments are to be removed, the cement has to dry for hours, especially if the attachment layer is

thick. The ostracode is then immersed in water, and the preparation is performed with needles especially ground for the purpose.

The preparation can be done with great precision, provided that the needle is kept steadily in motion during the entire procedure. The point of the needle is moved towards the particles to be removed until it touches them; if they do not fall away the next touches are made stronger or directed to other points on the particles. The particles are then removed with a fine jet of water from a syringe or a pipette, or brushed away with fine brushes the hairs of which have been cut down to 1–2 mm. The preparation generally takes less than half an hour, sometimes only some minutes, but a few specimens have required more than 20 hours of preparation.

Especially when larger fossil fragments are attached to the ostracodes the preparation becomes very tedious. They often leave a scar in the valve or carapace wall if they are removed, and it is, therefore, often better to clean and diminish them than to break them away. If a larger fragment has been in close contact with a valve and prevented its interior or a small sulcal space from being compactly filled with the argillaceous component of the matrix, calcite has crystallized or recrystallized there so that it cannot be separated from the ostracode shell. This is mostly the case with the crumina; even if it seems to be entirely filled with marl, this substance is so firmly cemented that it is impossible to get fine preparations of the interior of the crumina.

The ostracode is easily removed from the cement by immersion in acetone and is then washed once or twice in clean embryo dishes with acetone and can be photographed or prepared from another side.

Very often the ostracode is kept together by the matrix and will fall apart when freed from the cement. To prevent this they can be glued together with glues resistant to different solvents. The following system of two glues and two solvents has been used:

If the specimen is to be treated further with the preparation cement, the specimen is dried in the embryo dish before detachment and glued with a fairly weak tragacanth solution, applied so that it will be seen as little as possible on future photographs. It is then detached by means of acetone and can be handled as an entire specimen.

If the specimen is to be treated further with water or glued with tragacanth, the tragacanth is applied only along parts or one side of the cracks, and after detachment and washing in acetone as described above, the reparation can be completed with a weak acetone solution of cellulose acetate, and the ostracode be handled as an entire specimen in water solutions.

Though repaired specimens of this kind have generally been avoided, some examples have had to be figured (e.g. MARTINSSON 1960b, Pl. III, figs. 4–5, and this paper, Figs. 32 and 183B). Even individual broken spines can be restored in this way.

Concentrated alcohol can be used for rapid washing irrespective of which of the two glues has been used.

Photographing.—For this procedure the ostracodes have been mounted on glass slides with one of the two glues mentioned. Tragacanth usually gives a better natural background on the photograph, but cellulose acetate cement allows a better and more rapid orientation of the specimen and is somewhat more easily removed from it after photographing. The specimen is washed with alcohol which is blown away together with contaminating particles by means of a jet of dry air.

The specimen is then covered with a very thin layer of sublimated ammonium chloride. The ammonium chloride is heated in a short glass tube, preferably open at both ends. Pipette-like constrictions of closed tubes with ammonium chloride result in uncontrollable puffs of smoke, and the ostracode becomes unevenly and mostly too thickly covered with the sublimated ammonium chloride.

The photographing equipment used is a Leitz Aristophot II, mostly with a 42 mm Leitz Summar or a 40 mm Leitz Photar objective, mounted with a Leica camera for 24 × 36 mm negatives. The source of light has been a Bausch & Lomb Fluorescent Illuminator the light of which falls from the upper right corner, with white, yellowish, or silver-coloured paper reflectors placed about one centimetre from the ostracode on the other sides to weaken the shadows. The bellows have been arranged for negative scales of 10 ×, exceptionally 5 × or 20 ×. The film has invariably been Adox KB 14, 14°DIN. To obtain negatives for enlarging it has been found convenient not to stop the diaphragm further down than F : 12 or, possibly, F : 16. For the prints different Kodak Bromide WSG papers (hard, very hard, and normal) have been used.

Exact scales have sometimes been obtained by photographing an object micrometer scale on the first square of the film which allows checking even during the enlargement; generally, however, the magnification errors which might have occurred after further enlargement are negligible, but the all magnifications stated under the illustrations should, anyhow, be taken as approximate.

Measurements.—An ocular micrometer in a stereomicroscope has been used for the measurements. As a stereomicroscope gives parallactic errors, measurements have been made vertically in the field of view. The reading intervals with the scales used are 8.3 μ, except in Fig. 22 where the corresponding figures are 11.3 μ and 5.6 μ for different parts of the diagram (cf. Martinsson 1956, p. 4).

Stratigraphy and collecting localities

Current conceptions of the Silurian stratigraphy of Gotland and earlier references to *Beyrichiidae* from this sequence

The first review of the stratigraphic distribution of beyrichiids and other ostracodes on Gotland was given by Lindström (1888b) who listed 16 beyrichiid

species among which are 8 species ascertained to occur on Gotland, distributed according to the stratigraphical subdivision published by him in the same year (LINDSTRÖM 1888a). VAN HOEPEN (1910) gave a similar list and several locality records.

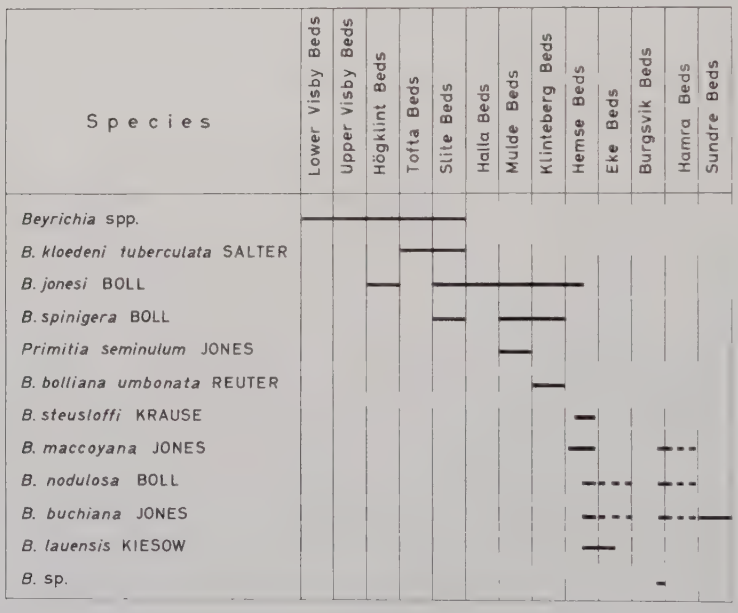
Our present conception of the stratigraphy of Gotland is largely founded on the works by HEDE (1921, 1925a and b, 1927a and b, 1928, 1929, 1933, 1936, 1940, cf. also MUNTHE 1921—all Geological Survey publications in Swedish—1942, 1958, and 1960, containing a key in English to the actual stratigraphy, pp. 44–52). The sequence above sea-level is subdivided into 13 units distinguished on "palaeontological-stratigraphical as well as petrographical basis" (cf. HEDE 1921, p. 27). They are, then, neither to be consistently regarded as biostratigraphic nor as lithostratigraphic units but received, long before conventions were introduced, formation and group names in close accordance with modern usage. Later the groups have been subdivided directly into members (cf. HEDE 1960), and generally the units not referred to as groups are without doubt of member size. The biotic evidence used for the subdivision should not, however, be underestimated, and HEDE's units have, therefore, been a most valuable framework for the palaeontological collecting work on which this study is based. In this connection it has been preferable not to rank the units or to group them together genetically, and for this reason they are neutrally termed "beds" below. Microfossil evidence, published here or unpublished, has not called for noteworthy revisions of the boundaries between these 13 units as defined by HEDE; on the contrary they are in several cases corroborated by the distribution of ostracodes. Further comments on the different units are added in connection with the locality list.

HEDE's descriptions to accompany the geological maps of Gotland contain abundant records on the occurrence of beyrichiid ostracodes. The number of species is restricted to ten, and it is generally easy to recognize the groups of ostracodes behind the consistently used specific names. As shown in Table 1 this subdivision in itself is enough to illustrate some of the more important changes in the beyrichiid faunas of Gotland.

BASSLER & KELLETT (1934) list more species from Gotland than recorded in the literature up to that date; this is due to the fact that GRÖNWALL's material from Scania (GRÖNWALL 1897, a paper in Swedish) has been referred to as coming from Gotland.

As the beyrichiid fauna at many of VAN HOEPEN's and HEDE's well defined localities is known in detail as a result of the present work, it is theoretically possible to include several individual references in the synonymy lists of the Descriptive Part. On the whole, however, this would lead to a very inconsistent treatment of the older papers, and the synonymy lists have been restricted to illustrations of correctly determined specimens and to taxionomical key papers. A general view of the synonymy can be obtained from the text to Table 1 and by comparison between this table and Table 2; furthermore several of the code names of localities below refer directly to localities described by HEDE.

Table 1. Stratigraphical distribution of beyrichiid ostracodes in the Silurian sequence of Gotland according to information in the descriptions to the geological maps (cf. p. 43). A certain synonymy can be reconstructed: *Beyrichia* spp. = *Beyrichiinae*, especially *Beyrichia halliana*, and *Craspedobolbininae*. *Beyrichia kloedeni tuberculata* = *Beyrichiinae*, especially *Beyrichia bicuspis*. *B. jonesi* = *Craspedobolbininae*, especially *Craspedobolbina unculifera*, *C. percurrens*, *C. clavata* and *C. robusta*. *B. spinigera* = *Beyrichiinae*, especially *Beyrichia dactyloscopica*, *B. morifera*, and *B. peponulifera* and possibly other species, as *B. snoderiana* and *B. contracta*. *Primitia seminulum* = *Bolbiprimitia inaequalis*, tecnomorphs. *B. bolliana umbonata* = probably *Beyrichia snoderiana*, *partim*. *B. steusloffi* = *Hammariella*. *B. maccoyana* = *Amphitoxotidinae*, especially *Hemsiella*, *Amphitoxotis*, *Hoburgiella*, and *Juviella*. *B. nodulosa* = *Neobeyrichia* spp. *B. buchiana* = *Neobeyrichia* spp., in the uppermost sequence with certainty *N. regnans*. *B. lauensis* = *B. lauensis*. *B.* sp. = *Cryptoloholobus ??*.



List and definitions of localities investigated

In order to avoid a complete definition of every locality in each of the numerous locality references in the following, short code names consisting of one or occasionally two words have been introduced and are defined below.

Fig. 14. Map of Gotland showing collecting localities and their code names as defined in the text, pp. 46–59. Halls huk, Fårö skola, and Lau backar are written according to English usage (Halls Huk, etc.) in the current text. The stratigraphical boundaries, according to J. E. Hede, have been drawn for a rough orientation as to the frequency and distribution of the localities within each unit (some minor lakes are drawn with inconsiderably thicker lines).

LOWER VISBY BEDS ○
UPPER VISBY BEDS ●
HÖGKLINT BEDS □
TOFTA BEDS ■
SLITE BEDS △
HALLA BEDS ▲
KLINTEBERG BEDS ◆
HEMSE BEDS ⊙
MULDE BEDS ◇
EKE BEDS ⊡
HAMRA BEDS ▽
BURGSVIK BEDS +
SUNDRE BEDS ▼
LOCALITY MAP
SCALE
0 5 10 15 20 km
Halls huk
Båta
Haganäs
Fårö skola
Oidehoburga
Brca
Stuks
Vastös
Irevik I
Lickershamn
Alby
Stora Banne
Puttarsjaus
Nyhamn
Nyhamn well
Längars
Kyllej
Hide
Spillings
Stora Myre
Yxne
Slite
Enholmen
Boge
Snäckgärdsbaden
Gustavsvik
Gane
Vike
Galgberget
Annelund
Visby I
Bingers
Käringen
Vallstena
Norrbys
Buske
Ygne
Follingbo
Stave
Bara
Hörsne
Nygårds
Gandarve
Gardrungs
Oivide
Möllbos
Gnisvärd
Ansarve
Sinnarve
Grogarns
Hammarudden
Hammars
Skåne
Haidby
Gannes
Fakle
Millklint
Valbytte
Klintebys
Hunninge
Svarvare
Klinte
Däpps
Mulde
Kaupungs
Sigvalde
Tänglings
Gogs
Botvide
Lau backar
Blåhäll
Djupvik
Amlings
Medbys
Linde
Gannor
Fie
Lerberget
Västarberget
Sandarve
Västlaus
Tjängdarve
Hägvide
Eske
Gläves
Snoder
Hulte
Vanges
Lukse
Leisungs
Halor
Petes
Hemmungs
Eke
Herrvide
Petsarve
Lingvide
Ronnings
Lunde
Sles
Gisle
Norrgårde
Husryggen
Hoburgen II a and b
Hoburgen I a and b
Juves

The names are found also on a locality map, Fig. 14. The names usually refer to the nearest place name on the geological map; sometimes (Annelund etc.) the distance to the nearest place name is so great that it cannot be expected to agree with local usage; in other instances (Gannor etc.) a new name has been given to an old locality (Lau Kanal, the canalized part of a brook system, is more ambiguous than Gannor). Closely situated localities have been distinguished by Roman numerals. The title of the geological map sheet is stated for each locality. As the map and locality list are also intended to be the locality key for subsequent publications based on the same field work it includes a couple of localities without determinable beyrichiids.

For each locality the numbers of the samples of very varying size (with the index letters MS, samples from 1961 not included) are also stated. The washed remainders of these samples will be deposited in the museum of the Palaeontological Institute, University of Uppsala, as extracted faunas or as partly unextracted finer fractions.

Lithological characteristics of the stratigraphical units and many localities are found in HEDE's descriptions to accompany the geological maps, and, easily accessible to the reader of English, in a summary by HEDE (1960, pp. 47–52). The current correlation with the international stratigraphy is found in the same paper; cf. HEDE 1942. A guide to the synonymy problems relative to the stratigraphical divisions used here and to names used 1888–1920 has also been compiled by HEDE (1925a, pp. 13–30, these lists have to be read in connection with the maps in Figs. 3–5 in HEDE 1921). Similar information for each of the stratigraphical units, with references to fauna and further literature is found in the *Lexique stratigraphique international* (HEDE 1958).

LOWER VISBY BEDS.—The microfauna confirms that these beds are palaeontologically considerably different from the Upper Visby Beds. The distinctness of the boundary has not been checked. At the Nyhamn well *Holophragma calceoloides* (LINDSTRÖM) is found together with the typical beyrichiid fauna of the Lower Visby Beds; it cannot be excluded, however, that the well begins in Upper Visby Beds.

NYHAMN.—Lummelunda sheet, parish of Lummelunda, shore exposure ca. 450 m NE of Nyhamns Fiskeläge. MS 17, 71, 78, 79, 83, 101, 176, 178, 182, 246, 391, 468, 469, and 470. *Apatobolbina simplicidorsata*, *Leptobolbina hypnodes*, *Craspedobolbina unculifera*, *C. juguligera*, *Barymetopon infantile*, *Noviportia simpliciuscula*, *Beyrichia halliana*, *B. hirsuta*.

NYHAMN WELL.—Lummelunda sheet, parish of Lummelunda, well immediately S of the road to Nyhamns Fiskeläge, ca. 200 m from the coast. MS 173. *Apatobolbina simplicidorsata*, *Leptobolbina hypnodes*, *Craspedobolbina unculifera*, *Noviportia simpliciuscula*, *Beyrichia halliana*.

GUSTAVSVIK.—Visby sheet, Visby, shore exposures immediately N and S of Gustavsvik. MS 25, 26, 53, 67, 94, 100, 129, 133, 138, 214, 252, 257, and 317. *Apatobolbina simplicidorsata*, *Leptobolbina hypnodes*, *Craspedobolbina unculifera*, *Noviportia*

simpliciuscula, Beyrichia halliana, B. hirsuta. Concomitant fauna: cf. Hede 1940, p. 12; 1960, p. 52 (Loc. 1).

Buske.—Visby sheet, parish of Västerhejde, shore cliff at Buske Fiskeläge. MS 192 and 343. *Apatobolbina simplicidorsata, Leptobolbina hypnodes, Craspedobolbina unculifera, Noviportia simpliciuscula, Beyrichia halliana.*

Upper Visby Beds.—Five species, including the important genus *Noviportia*, disappear, but only two new appear. The first rare primitiopsids, among them a small *Clavofabella* sp., appear. *Apatobolbina tricuspidata* has been found only in these beds.

Halls Huk.—Kappelshamn sheet, parish of Hall, coast cliff ca. 150 m SE of Halls Fiskeläge. MS 102 and 275. *Apatobolbina tricuspidata, Craspedobolbina juguligera, Beyrichia halliana.* Locality near the extreme right in Fig. 7, Hede 1933.

Irevik.—Kappelshamn sheet, parish of Stenkyrka, cliff ca. 500 m WNW of the fishing village (Flge) of Irevik. MS 13 and 288. *Apatobolbina tricuspidata, Craspedobolbina unculifera, Beyrichia halliana, B. bicuspis.*

Lickershamn I.—Lummelunda sheet, parish of Stenkyrka, coast cliff ca. 600 m NW of Ringvide. MS 305. *Craspedobolbina juguligera, C. unculifera, Beyrichia halliana, B. bicuspis.*

Snäckgärdsbaden.—Visby sheet, Visby "Södra Backen" at Snäckgärdsbaden. MS 428, 429, and 430. *Apatobolbina tricuspidata, Craspedobolbina juguligera, C. unculifera, Beyrichia halliana, B. bicuspis.* Locality figured by Hede 1940, Figs. 4–5; faunal list *ibidem*, p. 18; cf. Hede 1960, p. 55 (Loc. 3).

Ygne.—Visby sheet, parish of Västerhejde, ca. 150 m NE of the end of the road at Ygne Fiskeläge. MS 14 and 69. The material comes from a level earlier regarded as lowermost Högklint Beds; the only source of uncertainty in this respect is a broken tecnomorphic valve which could be an *Apatobolbina gutnica. Craspedobolbina juguligera, C. unculifera, Beyrichia halliana, B. bicuspis.*

Gnisvärd.—Klintehamn sheet, parish of Tofta, material excavated from the harbour (cf. Hede 1960, p. 73, Loc. 28). MS 35, 37, 42, 109, 142, 151, 152, 158, 175, and 181. *Apatobolbina tricuspidata, Craspedobolbina juguligera, C. unculifera, Beyrichia halliana.*

Högklint Beds.—It has been found practical to treat the lowermost member of these beds separately. The lithology, fauna, and facial differentiations of this member are described in detail by Hede 1940, pp. 18–22.

Lickershamn II.—Lummelunda sheet, parish of Stenkyrka, coast cliff ca. 500 m NW of Ringvide. MS 126 and 331 (lowermost member): *Apatobolbina gutnica, Craspedobolbina unculifera, Beyrichia halliana.* MS 324 (second member): *Apatobolbina gutnica* (?), *Craspedobolbina ornulata, Beyrichia halliana, B. hystricoides.* This sample belongs to the larger of the Högklint Beds columns in Table 2.

Visby I.—Visby sheet, Visby, road intersection of Kopparviksgatan and Gotevägen; small exposure between Kopparsviksgatan and the railway. MS 3, 46, 64, 70, 97, 248, 265, 266, 277, 289, 311, and 451. *Apatobolbina gutnica, Craspedobolbina unculifera, Beyrichia halliana, B. bicuspis.* Concomitant fauna: cf. Hede 1940, p. 22.

The higher parts of the Högklint Beds are very poor in marls—some marl pockets have proved to contain no palaeocopes at all and are not included here—which is especially unfortunate with respect to the fact that the Tofta

Beds offer quite a new aspect of the beyrichiid and primitiopsid faunas. The very marly locality of Ansarve, probably the youngest of the exposures of the Högklint Beds recorded here, has too poor a microfauna to reveal the quality of the contrast with the Tofta Beds. Large samples from Kanalen in Lummelunda, from the uppermost part of the Högklint Beds, yielded only *Leperditiocopa.*

Västös.—Kappelshamn sheet, parish of Hall, drainage ditch from Stormyr at the road ca. 1200 m SE of Västös. MS 39. *Craspedobolbina ? juguligera, C. unculifera, Beyrichia halliana, B. bicuspis.*

Irevik II.—Kappelshamn sheet, parish of Stenkyrka, uppermost marly beds on the reef flanks ca. 400 m WNW of the fishing village (Flge) at Irevik. Samples were taken at three different levels. The highest marl pocket (MS 386) did not contain determinable beyrichiids. The main part, from lower reef pockets (MS 93, 140, 184, and 345) contained *Craspedobolbina ornulata.* One sample, from the lowermost member of the Högklint Beds (MS 12) contained *Craspedobolbina unculifera* and *Beyrichia halliana.*

Visby II.—Visby sheet, Visby, the prominent cliff N of Gutevägen, between the railway and the Käringen windmill. MS 132, 207, and 406. *Craspedobolbina ornulata, Beyrichia halliana.*

Ansarve.—Klintehamn sheet, parish of Tofta, ditch by the W side of the small road ca. 350 m NW of Ansarve (SW of the habitation with this name). MS 440. *Beyrichia bicuspis.*

Tofta Beds.—One faunistic element, the *Bingeria* spp., appears and disappears again in this unit. The subfamily *Treposellinae* has its earliest representative here; the same is true for the genus *Clintiella.* The *Primitiopsinae* (*Clavofabella*) suddenly appear in great number. The samples are from the basal beds (Annelund, Galgberget) as well as from the upper part of the unit (Bingers).

Annelund.—Visby sheet, Visby, quarry W of the main road 1 km SW of Annelund. MS 50, 148, 171, 178, 194, 195, 199, 308, and 405. *Craspedobolbina mucronulata, C. unculifera, Beyrichia halliana, B. ponderosa, B. bicuspis, Bingeria zygophora, B. cyamoides.* Tecnomorphs of a *Saccarchites*-like form also appear, but the state of preservation does not allow a more detailed study. Hede (1940, Fig. 11) has published a photograph of a section very near to this locality.

Galgberget.—Visby sheet, Visby, quarry 300 m E of Galgberget. MS 449. *Beyrichia halliana, Beyrichia ponderosa, B. bicuspis, B. hystricoides, Bingeria zygophora.* A photograph of the E part of the section has been published by Hede (1940, Fig. 10); cf. Hede 1960, p. 55 (Loc. 4).

Bingers.—Visby sheet, Visby, quarry immediately SW of Bingerskvarn. MS 454. *Craspedobolbina unculifera, Clintiella bingeriana, Garniella* cf. *jugata, Beyrichia halliana, B. ponderosa, B. bicuspis, B. hystricoides, Bingeria zygophora, Bingeria cyamoides.* Cf. Hede 1960, p. 59 (Loc. 10).

Slite Beds.—It has been very difficult to make a consequent subdivision of the composite Slite Beds since the stratigraphical and facial conditions and the age relations of the members contained are far from clear. This especially concerns the large marly areas occupying a wide belt in the central part of the

outcrop of the Slite Beds. To treat the Slite Beds as one unit would, however, mean concealing important faunistic differences. In Table 2 the Slite Beds have been divided into three units, viz. (1) a lower part up to and including the beds with *Conchidium tenuistriatum*, (2) the central belt of marls, and (3) the uppermost limestone members east of this belt and some localities in the limestone cliffs or slopes west of it. With some further discussion the same disposition will be followed below. First some definitely early localities:

Käringen.—Visby sheet, Visby, old quarry (Hede 1940, Fig. 18), now almost completely filled in, between the Käringen windmill and Gutevägen. MS 450. *Beyrichia bicuspis*. Concomitant fauna and detailed description: cf. Hede 1960, p. 60 (Loc. 11).

Stora Myre.—Visby sheet, parish of Martebo, surface exposure (barren refrigeration ground) ca. 400 m WSW of Stora Myre. MS 34, 127, 145, 162, and 407. *Beyrichia halliana*, *B. bicuspis*, *B.* (aff. *Scabribeyrichia*) n.sp., *B. erinacea*. Though the *Beyrichiinae* are abundantly represented, no specimen at all of *Craspedobolbininae* has been found. Faunas from adjacent localities are listed by Hede 1940, pp. 48 and 49.

Yxne.—Visby sheet, parish of Lokrume, drainage ditch crossing the road ca. 700 m NE of Yxne Träsk, 150 m NW of the 43.96 m point. MS 38. *Craspedobolbina percurrens*, *Beyrichia halliana*, *B. bicuspis*.

Stora Banne.—Kappelshamn sheet, parish of Lärbro, cliff W of the road ca. 800 S of Stora Banne. MS 186 (further samples 1961). *Craspedobolbina perornata*, *Garniella jugata*, *Beyrichia halliana*, *B. bicuspis*.

Båta.—Fårö sheet, parish of Fårö, ditch 115 m E of the windmill E of Båta. MS 89 and 404. *Craspedobolbina perornata*, *C. mucronulata*, *C. percurrens*, *Beyrichia halliana*, *B. bicuspis*. *Conchidium tenuistriatum* Beds; concomitant fauna listed by Hede 1960, p. 70 (Loc. 24).

Stuks.—Kappelshamn sheet, parish of Bunge, excavation immediately SW of the coast road ca. 600 m NE of Stuks (Stux). MS 92. *Craspedobolbina mucronulata*, *Beyrichia halliana*.

The following five localities are from the SW part of the area, from a generally less calcareous facies with dark, grey marls. Sinnarve and Oivide are localities with the *Conchidium tenuistriatum* Beds, Valbytte is probably somewhat younger (*fide* Hede 1960, p. 73), and the only species from the Karlsö localities also occurs at Valbytte.

Sinnarve.—Klintehamn sheet, parish of Eskelhem, ditch 300 m SW of Sinnarve. MS 117. *Craspedobolbina sinnarvensis*, *Beyrichia halliana*. Concomitant fauna: cf. Hede 1960, p. 76 (Loc. 35).

Oivide.—Klintehamn sheet, parish of Eskelhem, quarry ca. 100 m W of the road and 100 m S of the raised beach 1100 m SW of Frändarve (parish of Stenkumla). MS 125. *Craspedobolbina sinnarvensis*, *C. percurrens*, *Beyrichia halliana*, *B. ponderosa*, *B. bicuspis*. Concomitant fauna: cf. Hede 1960, p. 76 (Loc. 36).

Valbytte.—Klintehamn sheet, parish of Sanda, ditches in a field ca. 500 m SSE of the southernmost house at Valbytte. MS 441 and 442. *Craspedobolbina sinnarvensis*, *C. insulicola*, *B. halliana*. Concomitant fauna: cf. Hede 1960, p. 73 (Loc. 29).

Lerberget.—Hemse sheet, parish of Eksta, Stora Karlsö, *Ketophyllum* Beds at Lerberget. MS 411, 412, 413, 414, and 415. *Craspedobolbina insulicola*. (Another

sample, from marly interbeddings in overlying limestones, 10–12 m below the main limestone sequence of the cliff, did not contain any ostracodes.)

Västarberget.—Hemse sheet, parish of Eksta, Västarberget (ca. 200 m south of the preceding locality). MS 390 and 425. *Craspedobolbina insulicola*.

The following localities have the typical Slite Marl fauna. The first known *Hollinidae* from Gotland appear. *Leptobolbina quadricuspidata* is often a characteristic element, though never very common. The characteristic broadly velate *Craspedobolbininae* and specialized *Beyrichiinae* found at several localities in the subsequent units are absent.

Follingbo I.—Visby sheet, parish of Follingbo, road cutting at the road intersection ca. 1250 m NW of the church of Follingbo. MS 18, 20, 47, 98, 244, 260, 268, 319, 321, 416, 419, and 435. *Leptobolbina quadricuspidata*, *Craspedobolbina percurrens*, *C. acuminulata*, *Garniella* sp., *Beyrichia ponderosa*, *B. bicuspis*, *B.* cf. *hellviensis* (not recorded in Table 2), *B. contracta*, *B. birupta*.

Follingbo II.—Visby sheet, parish of Follingbo, ditch immediately N of the road ca. 800 m S of the church of Follingbo MS 75, 306, and 420. *Craspedobolbina percurrens*, *C. acuminulata*, *Beyrichia halliana*, *B. bicuspis*, *B. ponderosa*, *B. contracta*, *B. birupta*.

Stave.—Visby sheet, parish of Akebäck, drainage ditch ca. 1500 m W of Stave. MS 74. *Craspedobolbina percurrens*, *Beyrichia contracta*. A list of the concomitant fauna from the same ditch section has been published by Hede 1940, pp. 59–60. This exposure was earlier regarded as one of the best in the Slite Marl; it is now densely overgrown.

Nygårds.—Klintehamn sheet, parish of Dalhem, canalized brook crossing the road at Nygårds. MS 191 and 201. *Craspedobolbina percurrens*, *C. cuspidulata*, *Beyrichia ponderosa*, *B. bicuspis*. Concomitant fauna listed by Hede (1927a, p. 30); *Pentamerus gotlandicus* Beds.

Vallstena.—Slite sheet, parish of Vallstena, ditch at the intersection with the road ca. 1100 m SSW of the church of Vallstena. MS 22, 65, 85, 326, 332, and 471. *Leptobolbina quadricuspidata*, *Craspedobolbina percurrens*, *C. cuspidulata*, *Beyrichia ponderosa*, *B. bicuspis*, *B. hellviensis*, *B.* aff. *morifera*. Concomitant fauna listed by Hede (1928, p. 23).

Vike.—Slite sheet, parish of Boge, ditch crossing the road of Vike. *Craspedobolbina percurrens*. Sample discarded owing to Quaternary contamination. Concomitant fauna listed by Hede (1928, p. 22).

Gane.—Slite sheet, parish of Bäl, railway section c:a 150 m NE of the halt of Gane. MS 323 and 458. *Leptobolbina quadricuspidata*, *Craspedobolbina percurrens*, *C. cuspidulata*, *C. acuminulata*, *Bolbiprimitia falculata*, *Beyrichia ponderosa*, *B. bicuspis*, *B. hellviensis*, *B.* aff. *morifera*, *B. contracta*.

Slite I.—Slite sheet, parish of Othem, quarry of the cement factory of Slite. MS 30 (7–8 uppermost meters of the section) and 32 (collected in material broken out from a lower level). *Leptobolbina quadricuspidata*, *Craspedobolbina percurrens*, *C. cuspidulata*, *C. acuminulata*, *Bolbiprimitia falculata*, *Beyrichia bicuspis*, *B. contracta*. Detailed description and concomitant fauna: cf. Hede 1960, p. 63 (Loc. 16).

Längars.—Kappelshamn sheet, parish of Hellvi, ditch crossing the road ca. 200 m N of Längars. *Leptobolbina quadricuspidata*, *C. percurrens*, *C. cuspidulata*, *C. acuminulata*, *Bolbiprimitia falculata*, *Beyrichia ponderosa*, *B. bicuspis*, *B.* ? *dactyloscopica*, *B. hellviensis*. Concomitant fauna: cf. Hede 1933, p. 47.

Hide.—Kappelshamn sheet, parish of Lärbro (exclave), cliff on the eastern shore

of Hidviken ca. 650 m WNW Hidtomt. MS 110, 160, 170, and 249. *Leptobolbina quadricuspidata, Craspedobolbina percurrens, Beyrichia ponderosa, B. bicuspis, B. hellviensis, B.* aff. *morifera.* Identical with the basal beds described in a section by Hede (1933, p. 53, with a fossil list).

Alby.—Kappelshamn sheet, parish of Rute, ditch crossing the road ca. 1200 m SSW of Alby. MS 253 and 263. *Leptobolbina quadricuspidata, Craspedobolbina percurrens, C. acuminulata, Beyrichia ponderosa, B. bicuspis, B. hellviensis, B. contracta, B. birupta.* Concomitant fauna: cf. Hede 1933, p. 48.

Oidehoburga.—Fårö sheet, parish of Fårö, small exposure (mainly consisting of wheel tracks) in a field ca. 250 m E of Oidehoburga (Åidehoburga). MS 177 and 245. *Beyrichia ponderosa, B. bicuspis.* The locality must be almost identical with one studied by Hede (1936, p. 30, with fossil list).

Fårö Skola.—Fårö sheet, parish of Fårö, shore ca. 600 m ENE of the church of Fårö (at Sk.h. on the map). MS 72, 114, 147, 185, and 262. *Craspedobolbina percurrens, C. cuspidulata, Beyrichia halliana, B. ponderosa, B. bicuspis, B. contracta, B. birupta.*

The following localities are situated on the slopes or in the cliffs W of the belt of Slite Marl. These localities show a faunistic transition towards the group of localities along the SE boundary of the outcrop of the Slite Beds. They are all in a much more calcareous facies than those in the preceding group, and it is difficult to establish to what extent the faunistic changes are due to facies differences. The Gardrungs locality, at least, which lacks the typical *Craspedobolbininae, Beyrichia* (*Asperibeyrichia*), and *Beyrichia* (*Scabribeyrichia*) of the higher beds, cannot be much younger than the *Conchidium tenustriatum* Beds. All localities contain Slite Marl elements.

Gardrungs.—Klintehamn sheet, parish of Eskelhem, low cliff NW of the road, opposite Gardrungs. MS 99 and 104. *Craspedobolbina percurrens, C. cuspidulata, Beyrichia ponderosa, B. bicuspis, B. hellviensis, B. contracta.*

Follingbo III.—Visby sheet, parish of Follingbo, roadside section ca. 600 m. W of Norrbys. MS 417. *Leptobolbina quadricuspidata, Craspedobolbina percurrens, C.* cf. *acuminulata, C. lativelata, Clintiella* sp., *Garniella biseriata, Beyrichia ponderosa, B. hellviensis, B. contracta, B. foliosa, B. birupta, B. apiculata.*

Norrbys.—Visby sheet, parish of Follingbo, excavation in the cliff ca. 400 m NNW of Norrbys. MS 418, 436, 437, and 438. *Craspedobolbina percurrens, C. cuspidulata, C. acuminulata, C. lativelata, Clintiella* sp., *Garniella biseriata, Beyrichia ponderosa, B. bicuspis, B. contracta, B. apiculata, B. birupta.*

Two localities on Fårö are younger than the Slite Marl there:

Haganäs.—Fårö sheet, parish of Fårö, shore cliff ca. 150 m NW of Haganäs. MS 445 (marly interbeddings in the middle member of the section) and 446 (Ryssnäs Limestone, not considered here owing to poor fauna). *Craspedobolbina percurrens, C. cuspidulata, Beyrichia halliana, B. bicuspis, B. hellviensis.* List of concomitant fauna and detailed locality description by Hede 1960, p. 71 (Loc. 25, middle member described).

Broa.—Fårö sheet, parish of Fårö, quarry and spring, ca. 2 km SE of the pier of Broa. MS 447. *Craspedobolbina percurrens, Beyrichia ponderosa, B. hellviensis.* List of concomitant fauna and detailed locality description by Hede 1960, pp. 71–72.

Six localities are from cliffs in the youngest Slite Beds. All of them are supposed to be younger than the *Pentamerus gotlandicus* Beds; Puttarsjaus

is probably somewhat older than the others. The faunistic component of broadly velate *Craspedobolbininae* also continues through the most calcareous parts of the following units.

Slite II.—Slite sheet, parish of Othem. Material from a small tube, RM No. Ar 26140, and six very small tubes in a larger one, RM Nos. Ar 26141–26146, only labelled "Slite". It must be regarded as certain, however, that the material described by Kiesow 1888 from "Quarnberget, Slite (h)" and Jones's (1888 b) material "from the uppermost strata of Slite" were separated from this collection. New collections from the cliff of Kvarnberget, however, have not yielded additional material. *Craspedobolbina percurrens*, *C.* cf. *lativelata*, *Aitilia* aff. *hyrsinicola*, *Clintiella hunningiana*, *Beyrichia ponderosa*, *B. bicuspis*, *B. hellviensis*, *B. foliosa*, *B. apiculata*.

Enholmen.—Slite sheet, parish of Othem, material from a tube, RM No. Ar 25888, labelled "Enholmen Slite". *Craspedobolbina percurrens*, *Clintiella hunningiana*, *Beyrichia ponderosa*. *B. bicuspis*, *B. hellviensis*, *B. foliosa*, *B. apiculata*.

Spillings.—Slite sheet, parish of Othem, cliff at the bend of the road at Spillings. MS 349. *Craspedobolbina percurrens*, *Beyrichia* sp. (small tecnomorphs).

Boge.—Slite sheet, parish of Boge, uppermost strata exposed in the quarries at the SE part of Boge Klint. MS 443. No beyrichiids.

Kyllej.—Kappelshamn sheet, parish of Hellvi, cliff at the 23.9 m point SW of Kyllej (Kyllaj). MS 299. *Craspedobolbina cuspidulata*, *Beyrichia bicuspis*, *B. apiculata*.

Puttarsjaus.—Kappelshamn sheet, parish of Hellvi, the cliff at the fishing village (Flge) ca. 500 m N of Puttarsjaus (Puttarsaus), eastern farm. Ms 118 and 120. *Craspedobolbina percurrens*, *C. acuminulata*, *Beyrichia* ? *dactyloscopica*, *B. bicuspis*.

In the SW part of the outcrop area of the Slite Beds, below the calcareous sandstone, the youngest Slite Beds consist of dark grey shales with a fauna showing some affinities to that in the overlying Mulde Beds. Owing to correlation difficulties in connection with the difference in facies it is not yet possible to establish their age relations to the preceding group of localities.

Svarvare.—Klintehamn sheet, parish of Klinte, ditch immediately E of the road NNE of Svarvare, ca. 1.5 km S of the road intersection at Klintehamn. MS 4, 56, 68, 123, 137, 143, 159, 270, 346, and 403. *Craspedobolbina simplicivelata*, *C. lunata*, *C. variolata*, *Beyrichia dactyloscopica*, *B. peponulifera*, *B.* aff. *morifera*. The fauna of this region has been subjected to a special study by Hede (1917), and the fauna in the present ditch exposure has been listed later by him (Hede 1927a, pp. 30–31).

Halla Beds.—Unfortunately only one locality in this interesting unit has yielded abundant beyrichiids.

Bara.—Slite sheet, parish of Hörsne and Bara, small quarries in the cliff of Bara Backe, ca. 300 m WSW of the church ruin of Bara. MS 460. *Craspedobolbina* sp. (cf. Hede 1960, p. 66, Loc. 19).

Gandarve.—Katthammarsvik sheet, parish of Dalhem, Dalhem rivulet ca. 100 m E of the watermill 400 m SE of Gandarve. MS 131, 144, 153, 163, 169, and 172. *Craspedobolbina percurrens*, *Beyrichia snoderiana*.

Hörsne.—Slite sheet, parish of Hörsne and Bara, drainage ditch immediately S of the church of Hörsne. MS 103, 478, 479, and 480. *Craspedobolbina percurrens*, *C. lativelata*, *Hyrsinobolbina hyrsinensis*, *Clintiella hyrsiniana*, *Aitilia hyrsinicola*, *Garniella* sp., *Beyrichia snoderiana*, *Beyrichia* cf. *morifera*, *B.* n.sp. (not referred to elsewhere).

Möllbos.—Klintehamn sheet, parish of Halla, bands of the rivulet ca. 50 m NW of the watermill of Möllbos. MS 444. Abundant *Beyrichia snoderiana*. Concomitant fauna: cf. Hede 1960 p. 67.

Mulde Beds.—The Mulde Beds have proved to be surprisingly heterogeneous as to the aspects of the ostracode faunas. However, the material from localities other than Mulde is not abundant and very difficult to work with, and on the whole the Mulde Beds are less thoroughly known than the other equally marly units.

Klintebys.—Klintehamn sheet, parish of Klinte, pond ca. 150 m SSW of the manor-house of Klintebys. MS 448. *Craspedobolbina clavata*, *Beyrichia dactyloscopica*.

Däpps.—Klintehamn sheet, parish of Klinte, railway cutting on both sides of the road-railway intersection at Däpps. MS 267, 273, 298, 301, 310, 399, 400, and 401. *Craspedobolbina percurrens*, *C.* cf. *clavata*, *Beyrichia dactyloscopica*, *B. snoderiana*, *B. altiplancta*.

Mulde.—Hemse sheet, parish of Fröjel, marl-pits of Mulde brickyard. MS 10 (originally consisting of about 85 part-samples of varying size) and 421. *Craspedobolbina clavata*, *Bolbiprimitia inaequalis*, *Beyrichia dactyloscopica*, *B. peponulifera*, *B. morifera*, *B. subornata*. Locality description by Hede 1927b, pp. 18–19; fauna list *ibidem*, p. 21; cf. Hede 1960, p. 74 (Loc. 31). The locality was earlier a well-known collecting-place for different fossils but is now very difficult of access (cf. Hede 1960, p. 74).

Blåhäll.—Hemse sheet, parish of Eksta, shore cliff immediately S of the parish boundary at Blåhäll. MS 463. *Craspedobolbina clavata*, *Beyrichia morifera*.

Djupvik.—Hemse sheet, parish of Eksta, cliff 400 m SW of Djauviks (Djupviks) Fiskeläge. MS 33, (121), 193, 344, 389 and 467. (*Craspedobolbina variolata*), *C.* ? *percurrens*, *C. clavata*, *Beyrichia dactyloscopica*, *B. morifera*.

Klinteberg Beds.—This unit is one of the most inaccessible on Gotland with respect to ostracode faunas in marls and is represented only by two samples from the beds containing *Conchidium biloculare*. The outcrop of the Klinteberg Beds constitutes the largest uninvestigated area in Fig. 14.

Hunninge.—Klintehamn sheet, parish of Klinte, quarry ca. 1 km SE of the manor-house of Klintebys. MS 8, 28, 36, 45, 146, 157, 164, 167, 168, 347, 472, 473, 474, 475, 476, and 477. *Craspedobolbina lembodes* (somewhat uncertain), *C.* cf. *lativelata*, *Aitilia calcarata*, *A.* cf. *calcarulata*, *Clintiella hunningiana*, *Garniella uniseriata*, *Beyrichia snoderiana*, *B. dactyloscopica*, *B.* cf. *morifera*.

Klinte.—Klintehamn sheet, parish of Klinte, NW corner of the cliff of Klinteberget, ca. 500 m NE of the church of Klinte. MS 111. *Garniella uniseriata*, *Beyrichia dactyloscopica*. Cf. Hede 1960, p. 75 (Loc. 34).

Hemse Beds.—As defined by Hede the Hemse Group consists of two main facies, one in the SW part of the outcrop area, another in the NE part. The boundary between these areas is stated by Hede 1927b, p. 24. If constructed independently and solely on the basis of the beyrichiid faunas, this boundary almost coincides with that given by Hede, if the disappearance of the genus *Craspedobolbina* is taken as datum, which is somewhat dangerous and not too orthodox from the methodological point of view. Thus drawn, the boundary

based on the microfauna will be consistently very slightly to the east of that based on the macrofauna.

In Table 2 these two main areas have been separated, and the zone separating the columns comes out as the most important faunistic boundary in the diagram. In the SW area the old Wenlockian *Craspedobolbina* (*Mitrobeyrichia*) and *Beyrichia* (*Beyrichia*) were still represented, together with only one representative of the *Amphitoxotidinae*, *Amphitoxotis curvata*. In the NE there was an explosive speciation in some genera, such as *Calcaribeyrichia*, *Neobeyrichia*, and *Beyrichia* (*Simplicibeyrichia*). The very differentiated *Amphitoxotidinae*, abundant in the Wenlockian of Britain but exclusively Ludlovian on Gotland, appeared in a great number of genera and species. Quite as pronounced are the changes in the undescribed primitiopsid faunas.

However, the picture is considerably more complicated. There is an important overlap of several faunistic elements, and the faunal successions show some compositional differences between the northern and the southern area of the NE "facies", "faunal area" (or time-unit?).

First are five localities in the typical SW facies:

Eske.—Hemse sheet, parish of Sproge, main drainage ditch from Mästarmyr, ca. 200 m from its western bend in Eske Träsk. MS 161 and 242. *Craspedobolbina percurrens, C. robusta, Amphitoxotis curvata, Beyrichia snoderiana.*

Snoder.—Hemse sheet, parish of Silte, main drainage ditch from Mästarmyr ca. 450 m SE of Botraifs. MS 150, 156, and 431. *Craspedobolbina percurrens, C. robusta, Amphitoxotis curvata, Beyrichia snoderiana.* Concomitant fauna illustrated by a list from a nearby locality by Hede (1927b, p. 26, lower list).

Lukse.—Hemse sheet, parish of Hablingbo, ditch crossing the road immediately S of the southern farm of Lukse. MS 81, 204, and 302. *Craspedobolbina percurrens, C. robusta, Neobeyrichia ? ctenophora* (only *Neobeyrichia* record in this facies).

Petes.—Hemse sheet, parish of Hablingbo, ditch ca. 650 m SW of Petes. MS 122 and 225. *Craspedobolbina percurrens, C. robusta, Amphitoxotis curvata.* Concomitant fauna listed by Hede (1960, p. 82, Loc. 44).

Hemmungs.—Hemse sheet, parish of Hablingbo, ditch in a field NE of the main road, ca. 100 m SE of the windmill at Hemmungs. MS 119. *Craspedobolbina percurrens, C. robusta, Beyrichia snoderiana.*

However, in a considerable area N and NW of Hemse a rare (and not always quite typical) *Craspedobolbina robusta* occurs together with elements both from the marls along the shore of Östergarn and from probably younger beds with *Neobeyrichia lauensis.*

Sandarve.—Hemse sheet, parish of Linde, marl pockets at the base of the cliff of the NE part of Sandarve Kulle. MS 15 and 66. *Craspedobolbina robusta.* Penecontemporaneous fauna listed by Hede (1927b, p. 34).

Linde.—Hemse sheet, parish of Linde, base of the cliff NW of the road passing the S part of the Lindklint and immediately NW of the church. MS 154. *Vinculoveliger catenulatus, Neobeyrichia lauensis.*

Amlings.—Hemse sheet, parish of Linde, ditch (canalized brook from Fride Träsk, Ramträsk, and Broträsk) ca. 650 m E of Amlings, 150 m S of the sharp bend.

MS 77, 155, and 304. *Craspedobolbina robusta, Hammariella pulchrivelata, Vinculoveliger catenulatus, Neobeyrichia nutans, N. lauensis.* A fauna list by HEDE (1927b, p. 26, upper list) must refer to practically the same locality.

TJÄNGDARVE.—Hemse sheet, parish of Hemse, ditch along the road 100 m E of the road-railway intersection. MS 259 and 261. *Craspedobolbina robusta, Hammariella pulchrivelata, Vinculoveliger catenulatus, Atterdagia paucilobata, Neobeyrichia ctenophora, N. nutans. N. lauensis.*

The area just described contains both *Craspedobolbina* and *Neobeyrichia lauensis* which is also characteristic of the last two groups of localities in the Hemse Bed discussed here. They also contain *Vinculoveliger* which occurs at one locality with elements from the Östergarn fauna but, though the material is abundant, without *Craspedobolbina* and *Neobeyrichia lauensis*:

MEDBYS.—Ronehamn sheet, parish of Lye, ditch immediately S of the road between Rotarve and Medbys, ca. 400 m SSW of Medbys. MS 105, 339, 396, 397, and 398. *Hammariella pulchrivelata, Vinculoveliger catenulatus, Neobeyrichia ctenophora, N. nutans.*

The northernmost locality in the Hemse Beds, at *Djupvik in Kräklingbo* (Katthammarsvik sheet, parish of Kräklingbo, northern shore of Djupvik, MS 91, 174, 180, 202, 203, and 205; cf. HEDE 1929, p. 27; not set down on the map) contains grey plastic clay below the beds with *Eurypterus fischeri* with abundant fossils embedded in thin layers; however, the calcareous matter of the ostracodes is damaged (the brachiopods are silicified), and the *Vinculoveliger* sp. and *Neobeyrichia* sp. found there could not be determined. In the Östergarn area a fauna with abundant *Calcaribeyrichia, Beyrichia* (*Simplicibeyrichia*), and occasional *Navibeyrichia hanseatica* and *Garniella lineolata* appears:

HAMMARUDDEN.—Katthammarsvik sheet, parish of Östergarn, southern part of the syncline marked on the map crossing the NW shore of Hammarudden. The samples are from three different levels, some meters apart, MS 196 in the lower, MS 124 and 136 in the middle, and MS 141, 183, 198, and 254 in the upper part of the section. Another sample, MS 9, is from the northern part of the syncline. *Garniella lineolata, Lauella* sp. (lowest level), *Grogarnia atlantica* (lowest level), *Beyrichia grogarniana, B. globifera, Calcaribeyrichia calcarata, C. simplicior, C.* cf. *simplicior* (lowermost level), *C. insignior* (lowest level), *Neobeyrichia nutans, Navibeyrichia hanseatica* (lowest level).

SKÅNE.—Katthammarsvik sheet, parish of Östergarn, shore at Skåne. MS 179 and 322. *Hammariella pulchrivelata, Calcaribeyrichia simplicior.*

GROGARNS.—Katthammarsvik sheet, parish of Östergarn, exposures in a small cliff (MS 24 and 54) near the shore, on the shore (MS 95 and 258) ca. 300 m SSE of Grogarnshuvud, and on the shore near the small point SSE of Grogarnslund (MS 38). *Beyrichia grogarniana, B. globifera, Calcaribeyrichia simplicior.* Concomitant faunas listed by HEDE 1929, pp. 31 and 32; cf. HEDE 1960, p. 77 (Loc. 38).

HAMMARS.—Katthammarsvik sheet, parish of Östergarn, excavation immediately SW of the Stora Hammars farm. MS 466. *Hammariella pulchrivelata, Beyrichia globifera, Calcaribeyrichia* sp., *Navibeyrichia hanseatica, Hexophthalmoides craterilobatus.*

In younger beds, in the cliffs of the same region, the new faunas become still more differentiated. The material, however, is not very abundant:

Gannes.—Katthammarsvik sheet, parish of Östergarn, cliff of Gannberget ca. 100 m SW of Gannes. MS 128, 197, 255, 461, and 462. *Beyrichia* n.sp., *B. globifera*, *Calcaribeyrichia calcarata*, *Gannibeyrichia* gannensis. The material is from different notches in the cliff figured by Hede 1929, Fig. 11.

Fakle.—Katthammarsvik sheet, parish of Östergarn, marl beds in the cliff of Kyrkberget W of the road ca. 350 m WNW of Fakle MS 139, 149, and 297. *Beyrichia* n.sp., *B. impersonalis*, *B. globifera*, *Calcaribeyrichia calcarata*, *Gannibeyrichia gannensis*.

Millklint.—Katthammarsvik sheet, parish of Gammelgarn, easternmost cliff of Millklint. MS 116, 279, and 341. *Calcaribeyrichia* sp. (fragmentary tecnomorph).

Haidby.—Katthammarsvik sheet, parish of Kräklingbo. Three tubes, RM Nos. Ar 25949, 25950, and 25951, labelled "Åker norr om Hejdeby Kräklingbo". *B. haidbyensis*, *B. globifera*, *B. callifera*.

The fauna from the lower levels of Östergarn can be followed towards SW with additions of new elements, reaching the *Craspedobolbina* area at the extreme SW locality:

Kaupungs.—Katthammarsvik sheet, parish of Ardre, northern cliff of Kaupungsklint ca. 200 m SSE of Mullvalds. MS 189. *Beyrichia grogarniana*.

Sigvalde.—Ronehamn sheet, parish of Etelhem, marl beds and pockets in the cliff ca. 300 m E of the 59 m point S of Sigvalde Träsk and near the quarry (figured by Hede 1925 b, Fig. 10) ca. 300 m SSW of this point. MS 134, 274, and 464. *Aitilia* cf. *calcarulata*, *Hammariella pulchricruminata*, *Beyrichia grogarniana*, *B. globifera*, *Calcaribeyrichia calcarata*, *C. simplicior*, *Navibeyrichia hanseatica*, *Hexophthalmoides* cf. *craterilobatus*.

Tänglings.—Ronehamn sheet, parish of Etelhem, road section E of the main road, opposite to and S of the intersection with the road to Tänglings (locality later destroyed in connection with road construction). MS 107, 329, 394, and 465. *Craspedobolbina robusta*, *Aitilia calcarata*, *Hamulinavis pirulifera*, *Garniella lineolata*, *G. strepuloides*, *Hammariella puchrivelata*, *Hemsiella pulchricruminata*, *Hoburgiella tenerrima*, *Beyrichia eteliana*, *Neobeyrichia ctenophora*, *Calcaribeyrichia caudata*, *C. simplicior*, *C. insignior*, *Navibeyrichia hanseatica*.

The combination *Neobeyrichia scissa – N. lauensis* is characteristic of the youngest faunas of the SE area. Some localities can be regarded as transitional (cf. Tjängdarve, etc.):

Hulte.—Hemse sheet, parish of Hemse, small ditch immediately N of the road ca. 1 km ENE of Hulte. MS 1, 55, 73, 217, 228, 290, and 292. *Sleia equestris*, *Hemsiella hemsiensis*, *Hoburgiella tenerrima*, *Atterdagia paucilobata*, *Lophoctenella* cf. *scanensis*, *Neobeyrichia scissa*, *N. lauensis*.

Leisungs.—Hemse sheet, parish of Havdhem, excavation S of the main road 200 m E of Havdhemhavor, between the road to Leisungs and the parish boundary. MS 294 and 342. *Hemsiella hemsiensis*, *Neobeyrichia scissa*.

Fie.—Ronehamn sheet, parish of Lau, ditch along the field road to Nybygget, ca. 350 m E of Fie (southern farm with this name, ca. 200 m N of the Lau-När parish boundary). MS 76 and 236. *Hammariella pulchrivelata*, *Atterdagia paucilobata*, *Lophoctenella* cf. *scanensis*, *Neobeyrichia scissa*, *N. lauensis*.

At most remaining localities only the two *Neobeyrichia* species have been found:

Vanges.—Ronehamn sheet, parish of Burs, ditch section immediately NE of the road ca. 300 m NNW of Vanges. MS 226. *Neobeyrichia scissa, N. lauensis.*

Gläves.—Ronehamn sheet, parish of Burs, excavation N of the road immediately W of the western farm at Stora Gläves. MS 229 and 295. *Neobeyrichia scissa, N. lauensis.*

Hägvide.—Ronehamn sheet, parish of Burs, several small ditches in the fields immediately N of the road, half-way between Hägvide and Häffride. MS 5, 82, 230, 235, 284, and 291. *Hammariella pulchrivelata, Neobeyrichia scissa, N. lauensis.*

Gannor.—Ronehamn sheet, parish of Lau, southern part of the Lau Kanal section (Hede 1925b, layer *b* in Fig. 19; cf. pp. 37–38). MS 48. *Neobeyrichia scissa, N. lauensis.*

Gogs.—Ronehamn sheet, parish of Lau, ditch in the field ca. 350 m NNW of Gogs. MS 243, 276, and 278. *Neobeyrichia scissa, N. lauensis.* Concomitant fauna listed by Hede 1960, pp. 79–80 (Loc. 41). The beds with a conglomeratic appearance described by Hede (l.c.) have proved to contain fairly abundant vertebrate remains, among them probably the oldest acanthodians known ("*Gomphodus*" sp.; det. T. Ørvig); these beds occur interbedded with shales containing the two ostracodes mentioned.

Botvide.—Ronehamn sheet, parish of Lau, low cliff in Lau Backar immediately W of the road at the southern farm of Botvide (cf. Hede 1925b, p. 45). MS 87, 96, 213, 218, 219, and 286 (layer *b*, Hede, l.c.) and MS 108 (layer *e*, Hede, l.c., with the same fauna). *Sleia equestris, Lophoctenella* cf. *scanensis, Neobeyrichia scissa, N. lauensis Plicibeyrichia* aff. *ornatissima.* Locality description also by Hede 1960, p. 80 (Loc. 42).

Eke Beds.—In contrast to the Hemse Beds, the Eke Beds have proved to be very little faunistically differentiated. An exception is the first locality which has an abundant fauna with some affinities to the Hemse Beds by containing the last *Craspedobolbininae*:

Lau Backar.—Ronehamn sheet, parish of Lau, temporary pool with exposures of weathered marly limestone at the summit of Lau Backar, ca. 650 m E of Hallbjäns. MS 16, 19, 40, 51, 88, 211, 212, 215, 227, 234, 241, 395, 408, 409, 410, 455, 456, and 457. *Aitilia calcarulata, Hamulinavis convexivelata, Clintiella* cf. *hyrsiniana, Garniella* sp., *Retisacculus commatatus, Sleia equestris, Hemsiella loensis, H. anterovelata, Lauella uncinata, Beyrichia globifera, B. duplicicalcarata, Neobeyrichia ctenophora, Calcaribeyrichia bicalcarata, Plicibeyrichia ornatissima, Gannibeyrichia biplicata, Kolmodinia* cf. *grandis.*

The Eke Beds at *Gannor* (MS 23, 27, 58, 385, and 387; locality defined under the Hemse Beds) did not contain any beyrichiids. The other localities are in dark grey calcareous shales, generally with abundant "*Sphaerocodium gotlandicum*".

Halor.—Ronehamn sheet, parish of Rone, excavation immediately NE of the road at Halor, ca. 300 m S of Ronehamn railway station. MS 313 and 327. *Sleia equestris, Hemsiella loensis, Neobeyrichia ctenophora.*

Eke.—Hemse sheet, parish of Eke, excavation immediately SE of the road, at the 23.99 m point E of the church of Eke. One small sample, MS 135. *Sleia equestris, Neobeyrichia ctenophora.*

Herrvide.—Hemse sheet, parish of Eke, ca. 2 km SE of the church, excavation immediately NW of the road at the corner of the parish boundary at Herrvide. MS 340. *Sleia equestris, Hemsiella loensis, Neobeyrichia ctenophora.*

Petsarve.—Hemse sheet, parish of Eke, excavation in a field between the farms and the two windmills at Petsarve, near the 15.2 m point. MS 115, 300, 333, 336, and 348. *Sleia equestris, Neobeyrichia ctenophora.*

Lingvide.—Bergsvik sheet, parish of Havdhem, excavation immediately NE of the road ca. 250 m SE of the railway–road intersection. MS 6, 57, 307, 312, 330, 334, and 335. *Sleia equestris, Neobeyrichia ctenophora, N. scissa.*

Ronnings.—Burgsvik sheet, parish of Grötlingbo, ditch crossing the road ca. 250 m S of Ronnings. MS 221, 303, 314, and 315. *Sleia equestris, Hemsiella loensis, Neobeyrichia ctenophora, N. scissa, N. lauensis.*

Burgsvik Beds.—Only very locally in the upper part of this unit, associated with the oolitic beds immediately below the beds with abundant *Pteronitella retroflexa*, have sandy marls containing beyrichiids been found. There is no distinct faunistic boundary towards the Hamra Beds which, furthermore, retain many of the faunistic and lithological characteristics of the Eke Beds. The Burgsvik Beds probably represent only a short episode in the sedimentation history of the Silurian of Gotland.

Husryggen.—Burgsvik sheet, parish of Sundre, quarries 300–500 m SSW of Husryggen. MS 21, 44, 112, 206, 210, 238, 269, 296, and 422. *Hoburgiella tenerrima, Cryptolopholobus semilaqueatus, Neobeyrichia ctenophora.*

Hamra Beds.—The Burgsvik Beds grade more or less indistinctly into the beds with "*Sphaerocodium gotlandicum*" of the Hamra Beds. These contain some components of the "*Sphaerocodium*" beds in the Eke Beds but also some new elements appear:

Lunde.—Burgsvik sheet, parish of Grötlingbo, quarries ca. 500 m E of the road intersection at Lunde. MS 392. *Sleia equestris, Hemsiella loensis, Hoburgiella tenerrima, Neobeyrichia ctenophora, Calcaribeyrichia bicalcarata, Plicibeyrichia ornatissima.*

Sles.—Burgsvik sheet, parish of Grötlingbo, quarry ca. 150 m E of the main road S of Sles, about 200 m SSE of Uddvide. MS 80, 86, 130, 239, 309, 393, and 423. *Sleia equestris, Retisacculus semicolonatus, Hemsiella loensis, H. anterovelata, Cryptolopholobus semilaqueatus, Calcaribeyrichia bicalcarata, Plicibeyrichia ornatissima.* Cf. Hede 1960, p. 83 (Loc. 46).

Gisle.—Burgsvik sheet, parish of Öja, ditch between the windmill and road intersection S of Gisle. *Treposellinae* indet., *Beyrichia barbulimentata, Calcaribeyrichia bicalcarata.*

Norrgårde.—Burgsvik sheet, parish of Hamra, two tubes, RM Nos. Ar 26062 (labelled "Norrgårda Hamra") and Ar 26064 (labelled "Ur en brunn"—from a well—"Norrgårda Hamra"). *Calcaribeyrichia bicalcarata, Navibeyrichia balticivaga.*

Hoburgen.—(Not set down on the map.) Basal Hamra Beds below Hoburgen II a (1961) *Sleia equestris, Beyrichia barbulimentata, Calcaribeyrichia bicalcarata.*

A series of samples are from reef pockets and in marly deposits distally of the reefs in the upper part of the Hamra Beds:

Hoburgen Ia.—Burgsvik sheet, parish of Sundre, southern and western cliffs of the southernmost clint, Storburgen ("Första Burg") in the Hoburgen complex. A

series of samples are from the notch immediately above the screes and below the Hoburg "Marble" (section figured by MUNTHE 1921, Fig. 36). Samples have been taken at different distances from the reefs at the western end of the notch, MS 188 and 316 near the reefs, MS 90 in the middle part of the section, MS 247, 250, 256, and 264 in its eastern part. Unspecified samples MS 7, 41, and 43. From pockets in the reefs in the western cliff come MS 402, 426, 427, and 459; MS 165 and 439 come from excavations in the clint. *Retisacculus* cf. *commatatus*, *Sleia equestris*, *Hemsiella loensis*, *Hoburgiella tenerrima*, *Juviella juvensis*, *Lophoctenella angustilaqueata*, *Neobeyrichia ctenophora*, *N. regnans*.

The excavated material also contains beds with conglomeratic appearance, similar to those at Gogs, containing abundant vertebrate remains.

HOBURGEN IIa.—Burgsvik sheet, parish of Sundre, the "second" clint of Hoburgen. Marly beds in and below the reef figured by MUNTHE 1921, Fig. 40. MS 2, 49, 113, 222, 237, 240, 251, 271, 272, 280, 282, 283, 285, 287, and 318). *Garniella* sp. (not discussed elsewhere), *Retisacculus* cf. *commatatus*, *Sleia equestris*, *Hemsiella loensis*, *Hoburgiella tenerrima*, *Lophoctenella angustilaqueata*, *Juviella juvensis*, *Beyrichia barbulimentata*, *Neobeyrichia protuberans*, *N. regnans*.

HOBURGEN IIb.—Burgsvik sheet, parish of Sundre, the "second" clint of Hoburgen. Slightly lower level than Hoburgen IIa. Marly beds in a cave figured by MUNTHE 1921, Fig. 35. MS 31, 220, and 232. *Retisacculus* cf. *commatatus*, *Sleia equestris*, *Hemsiella loensis*, *Hoburgiella tenerrima*, *Lophoctenella angustilaqueata*, *Cryptolopholobus semilaqueatus*, *Beyrichia barbulimentata*, *Neobeyrichia regnans*.

SUNDRE BEDS.—As far as the ostracode faunas are concerned there is no basis for a distinction between the Hamra and Sundre Beds as biostratigraphical units.

HOBURGEN Ib.—Burgsvik sheet, parish of Sundre, summit of Storburgen. Three marl pockets in the Hoburg "Marble". MS 208 and 320 in a more thinbedded limestone at the southernmost end of the clint. MS 166, 200, 325, and 337 are from the southeasternmost corner of the "marble" quarry; MS 106 is from the southern wall of the same quarry. *Retisacculus* cf. *commatatus*.

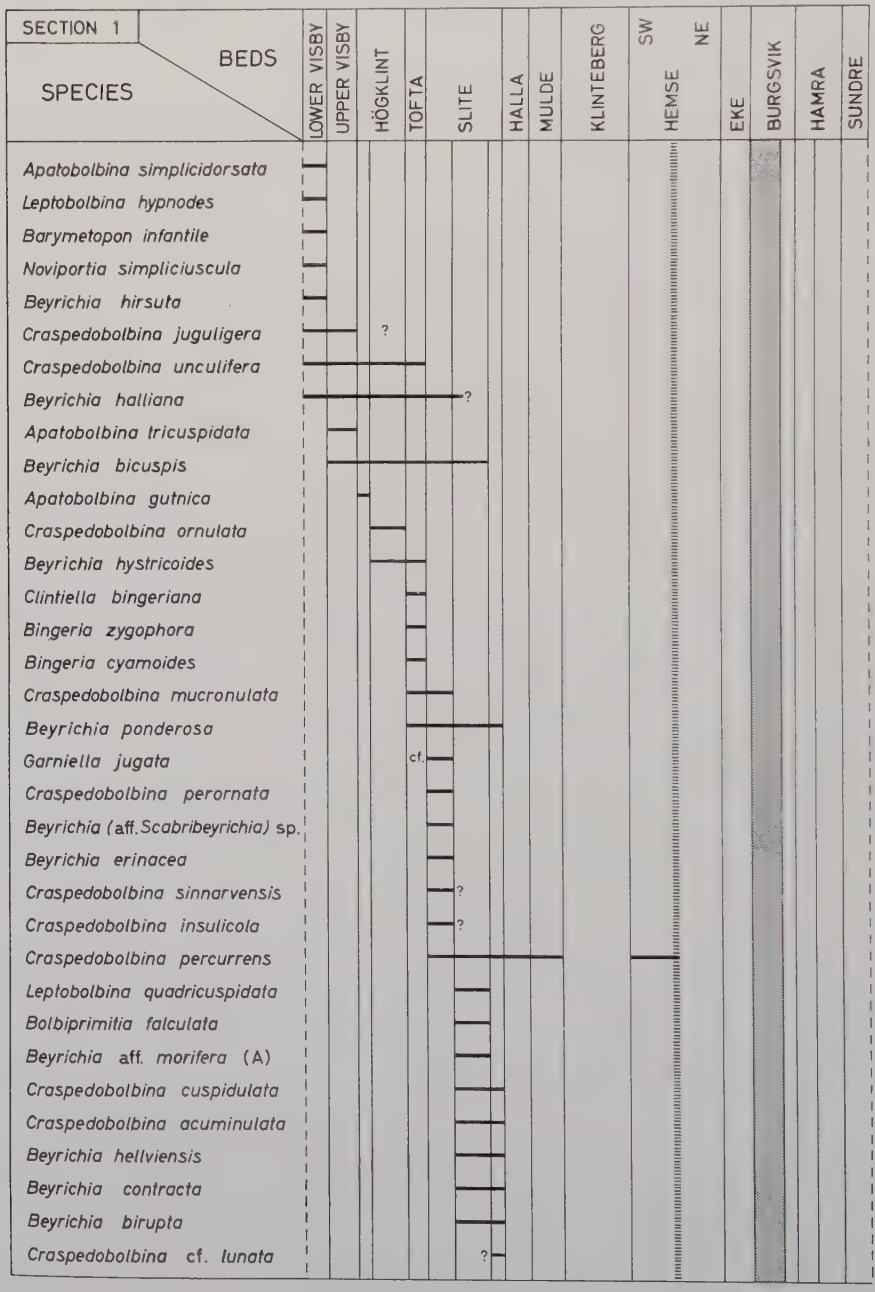
JUVES.—Burgsvik sheet, parish of Sundre, the cliff immediately NW of the main road, S of the dip indication on the geological map ca. 100 m W of Juves. MS 84, 233, and 452 (from the lower part of the section); MS 231, 281, 293, and 453 (from different higher levels in the section). *Sleia equestris*, *Hemsiella loensis*, *Hoburgiella tenerrima*, *Juviella juvensis*, *Beyrichia barbulimentata*, *Plicibeyrichia ornatissima*, *Neobeyrichia ctenophora*, *N. regnans*.

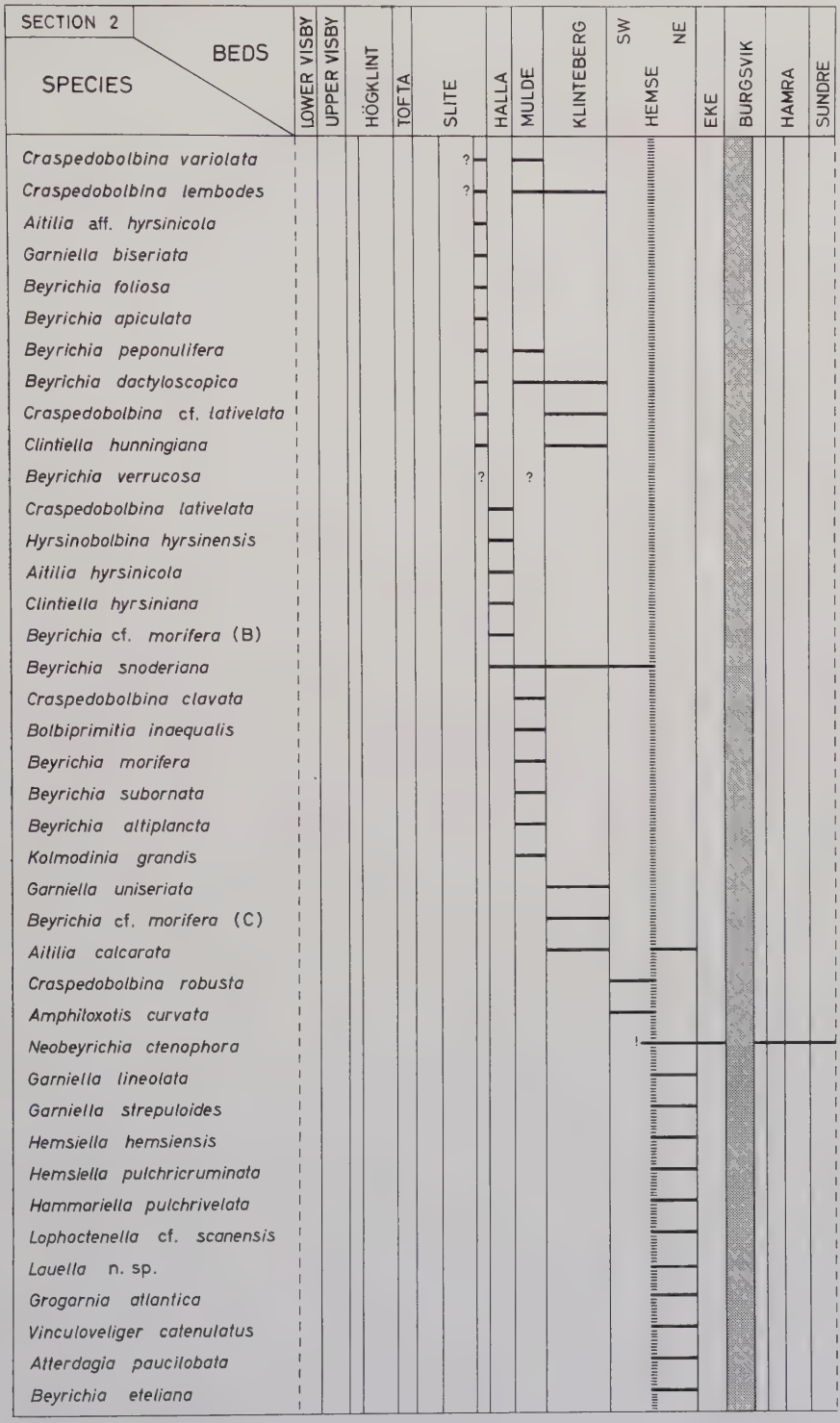
Comments to a new table of the distribution of beyrichiids in the Silurian sequence of Gotland and remarks as to its construction

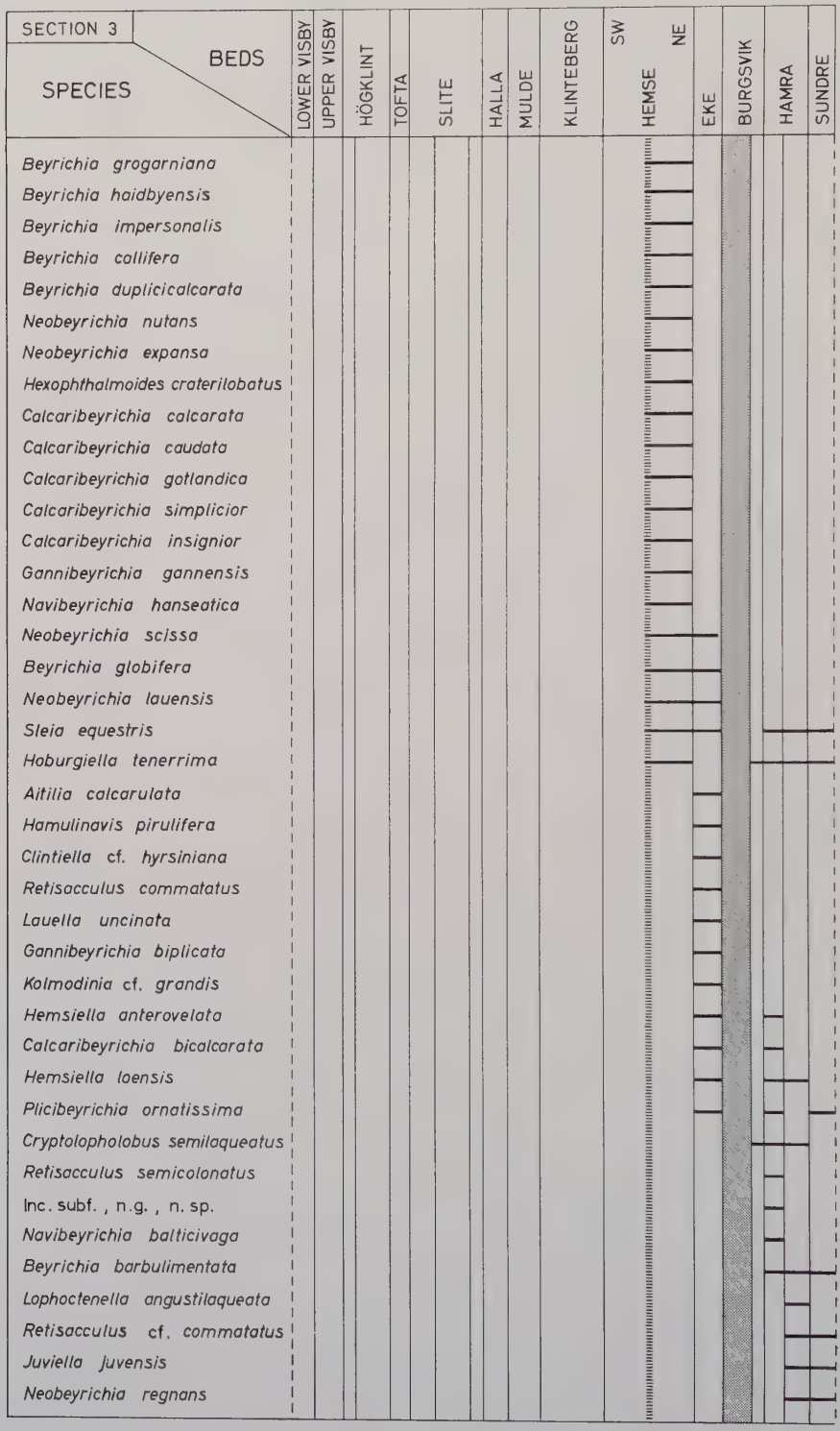
Table 2 presents, in a very peremptory way, the stratigraphical distribution of the *Beyrichiidae* in the Silurian sequence of Gotland. Some explanatory notes must be added.

The columns representing the stratigraphical units have been varied in order to give a rough idea of the relative thickness of each unit; it is, however, technically impossible to vary the width of the columns so that they are consistently proportional to the thickness of the units represented by them.

Table 2. Stratigraphical distribution of beyrichiid ostracodes in the Silurian sequence of Gotland. Simplified compilation of the references in the locality list and in the descriptions of the species. Stratigraphical units according to HEDE, as used in the descriptions to the geological maps of Gotland, with major subdivisions as referred to in the locality list. Distribution between the vertical lines in the table generalized except for a few cases.




SECTION 2
BEDS
SPECIES
LOWER VISBY
UPPER VISBY
HÖGKLINT
TOFTA
SLITE
HALLA
MULDE
KLINTEBERG
SW
HEMSE
NE
EKE
BURGSVIK
HAMRA
SUNDRE
Craspedobolbina variolata
Craspedobolbina lembodes
Aitilia aff. hyrsinicola
Garniella biseriata
Beyrichia foliosa
Beyrichia apiculata
Beyrichia peponulifera
Beyrichia dactyloscopica
Craspedobolbina cf. lativelata
Clintiella hunningiana
Beyrichia verrucosa
Craspedobolbina lativelata
Hyrsinobolbina hyrsinensis
Aitilia hyrsinicola
Clintiella hyrsiniana
Beyrichia cf. morifera (B)
Beyrichia snoderiana
Craspedobolbina clavata
Bolbiprimitia inaequalis
Beyrichia morifera
Beyrichia subornata
Beyrichia altiplancta
Kolmodinia grandis
Garniella uniseriata
Beyrichia cf. morifera (C)
Aitilia calcarata
Craspedobolbina robusta
Amphiloxotis curvata
Neobeyrichia ctenophora
Garniella lineolata
Garniella strepuloides
Hemsiella hemsiensis
Hemsiella pulchricruminata
Hammariella pulchrivelata
Lophoctenella cf. scanensis
Lauella n. sp.
Grogarnia atlantica
Vinculoveliger catenulatus
Atterdagia paucilobata
Beyrichia eteliana


SECTION 3
BEDS
SPECIES
LOWER VISBY
UPPER VISBY
HÖGKLINT
TOFTA
SLITE
HALLA
MULDE
KLINTEBERG
SW
HEMSE
NE
EKE
BURGSVIK
HAMRA
SUNDRE
Beyrichia grogarniana
Beyrichia haidbyensis
Beyrichia impersonalis
Beyrichia callifera
Beyrichia duplicicalcarata
Neobeyrichia nutans
Neobeyrichia expansa
Hexophthalmoides craterilobatus
Calcaribeyrichia calcarata
Calcaribeyrichia caudata
Calcaribeyrichia gotlandica
Calcaribeyrichia simplicior
Calcaribeyrichia insignior
Gannibeyrichia gannensis
Navibeyrichia hanseatica
Neobeyrichia scissa
Beyrichia globifera
Neobeyrichia lauensis
Sleia equestris
Hoburgiella tenerrima
Aitilia calcarulata
Hamulinavis pirulifera
Clintiella cf. hyrsiniana
Retisacculus commatatus
Lauella uncinata
Gannibeyrichia biplicata
Kolmodinia cf. grandis
Hemsiella anterovelata
Calcaribeyrichia bicalcarata
Hemsiella loensis
Plicibeyrichia ornatissima
Cryptolopholobus semilaqueatus
Retisacculus semicolonatus
Inc. subf., n.g., n. sp.
Navibeyrichia balticivaga
Beyrichia barbulimentata
Lophoctenella angustilaqueata
Retisacculus cf. commatatus
Juviella juvensis
Neobeyrichia regnans

A species known from a part of a unit is recorded with a line across the whole corresponding column. Time-lines cannot be drawn through the sequence of Gotland in such a manner that a more differentiated system could be made consistent.

In the Slite and Hemse beds the rough subdivisions made are based on very imperfectly known facial or stratigraphical conditions, or combinations of them. In the Slite Beds the faunistic overlaps do not lead to more serious contradictions in comparison with the text if the simplified boundaries are drawn as lines; in the Hemse Beds it has been necessary to let the faunas overlap in a ruled zone.

All these conditions tend to make the faunistic boundaries more pronounced than is verified by detailed studies. They are further emphasized by the fact that the beginning or the end of the range of a species or a fauna might be cut by one of the thick limestone units. As far as has been checked hitherto, however, the limestone members are not expected to surprise as to the stratigraphical ranges.

The present study has had as its purpose to describe the faunas and to provide as detailed background as possible for the conception of the beyrichiid system presented here. This has been achieved by making use of abundant faunas at scattered localities. For a more differentiated picture than that presented in Table 2 it is necessary to work through continuous sections, including also the limestones. I might seem discouraging to do this with the beyrichiids the systematics of which is so dependent on ventral structures which are difficult to expose. However, the specific characters are predominantly associated with the lateral surfaces of the valves which are even more cleanly exposed, without tedious preparation, when found on limestone surfaces. Once known, the developmental lines in the ventral morphology can also be followed into new branches exhibited by genera known only from limestone material (e.g. the *Kloedeniinae*); nor are the difficulties of preparation by any means insuperable.

GENERAL PART

Morphology and terminology of the beyrichiid carapace

Terminological principles

The terminology used for the description of fossil ostracode carapaces is far from reaching stability. The most ambitious attempt in this direction is the synopsis by Kesling (1951) in which the terminological usage of a number of authors between 1869 and 1948, writing in different languages of different groups of ostracodes, was analysed and used as the basis for a normalized and consistent set of terms. In subsequent papers on palaeocopes, however,

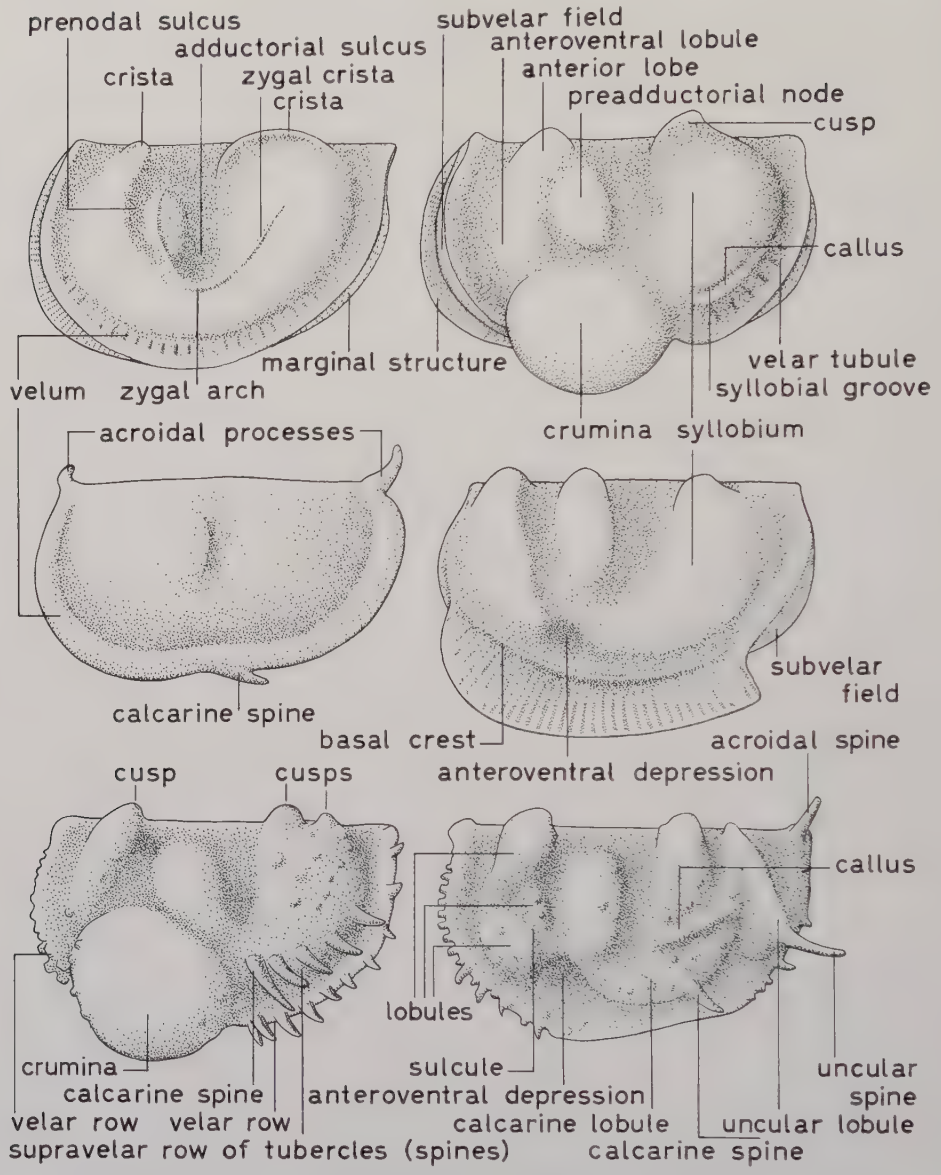


Fig. 15. Terminology of the beyrichiid carapace.

especially those by HENNINGSMOEN (1953), MARTINSSON (1955), JAANUSSON (1957), and MARTINSSON (1960b and c), new terms with bearings on the present study have been added. JAANUSSON's paper (op. cit.) implies a reconsideration of the entire palaeocope terminology and a synthesis of a term system for the adventral structures and the dimorphic features associated with them.

Two basic principles in this connection are that a revised terminology should be based as firmly as possible in existing terminological tradition and that it should be as widely applicable as possible within the major systematic group concerned. However, this often conflicts with two other basic needs. It is impossible to form consistent and homogeneous term systems on the basis of terminological priority, and if a terminology is too widely applied it often leads to false homologies and false genetic associations. This complex of problems has mostly to be solved by a compromise, and in practice there is generally no disagreement on this point.

Terms should not, however, be selected among words in common everyday speech. Further, it should be possible to translate them to and from different languages by using the same stems and to recognize them without difficulty in a foreign text. As most European languages, including all "Congress" languages, have well-established rules for adopting Latin words, this is best achieved by using Latin or latinized stems for terms in the strict sense. Native words with a very wide and indefinite application, such as list, flange, strip, knob, etc., which are needed for the natural flexibility of the descriptive language, should not be confined as true terms for one specialized structure only. In this respect practice varies considerably.

The superfamily *Beyrichiacea*, the suborder *Palaeocopa*, and the order *Beyrichiida*, as introduced by Ulrich & Bassler (1923), Henningsmoen (1953), and Pokorný (1953), respectively, are all founded on a conception that the family *Beyrichiidae* is most representative for the new group formed. It is, however, the most obviously specialized branch of the palaeocope system. In spite of this, it is not too inconvenient as a basis for a morphological terminology for palaeocopes, as primitive beyrichiids have their essential lobal features and even adventral structures in common with primitive forms in obviously closely related superfamilies. In this paper, therefore, the general applicability of the terminology is restricted to the *Palaeocopa*, and it has been found premature to construct any homologies between this specialized group and recent ostracodes, as, e.g., directly between the radial pore canals or the zone of concrescence of the *Podocopa* and any features in the *Palaeocopa*.

The emendations of or additions to current terminology and nomenclature in this paper, in order to reach further towards a consistent, more stringent, and interlingual usage, are further discussed below.

Contact conditions of the valves

Hinge.—The articulating part of the margin of the valves is straight. The hinge mechanism is very simple and comparatively little varied within the family. Basically, it consists of a groove in the right valve, with a corresponding ridge in the left valve. However, in the middle of the groove there is a more or less pronounced ridge, and at least towards the anterior end the ridge of the left valve is divided into two parallel ridges separated by a narrow furrow. The hinge elements are, then, *two parallel grooves in the right valve*, somewhat broader towards the cardinal corners, articulating with *a ridge in the left valve, divided, at least towards the anterior end, into two parallel branches*, somewhat thickening towards the cardinal corners (Figs. 16 and 20).

These conditions, described here as occurring in the genus *Craspedobolbina*, were studied by Pokorný in 1959 on material from Mulde on Gotland. He

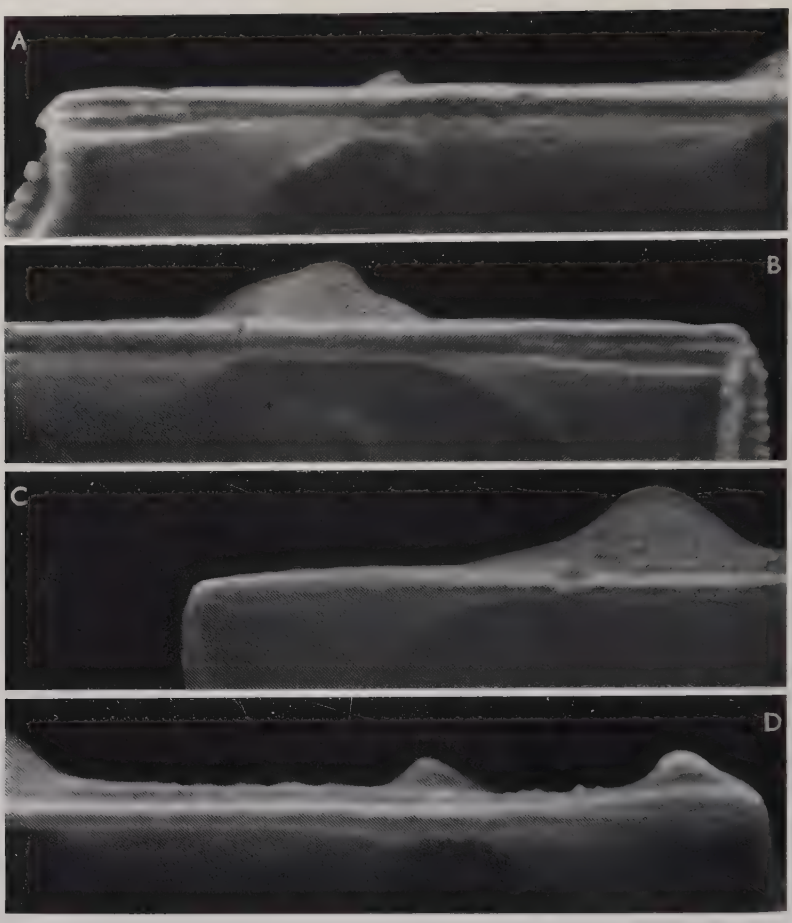


Fig. 16. Hinge mechanism in *Craspedobolbina* (*Mitrobeyrichia*) *clavata* (Kolmodin). A–B. Overlapping photographs of the groove complex of a right valve, No. G 269. C–D. Corresponding photographs of the ridges of a right valve, No. G 270. A–D ×75.

also stressed that there is a difference between the genus *Craspedobolbina* (then *Mitrobeyrichia*) and *Beyrichia* as to the construction of the hinge; in the latter genus the ventral groove breaks through the ventral ridge inside the valves at the cardinal corners, and the ventral groove is proportionally larger.

Pokorný's aspects of the hinge mechanism are founded on elaborate homologizations of the flange, selvage, and list along the duplicature of recent ostracodes on one side and the ridges of the beyrichiid hinge on the other, *via* the conditions along the contact margin as exhibited by the beyrichiids. The contact conditions of the valves are, however, strongly specialized functionally, and it does not seem a very natural way to interpret the construction of the hinge starting from the presumption that the beyrichiid carapace has passed a stage of case-in-case arrangement of two even more asymmetric valves.

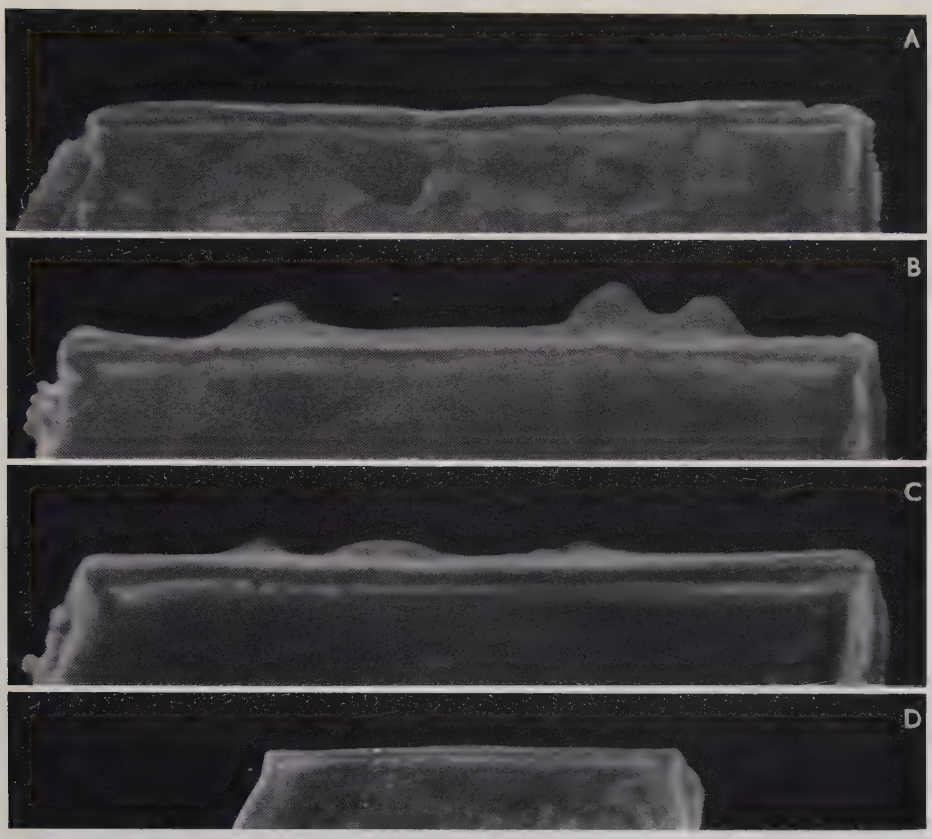


Fig. 17. The groove complex constituting the hinge mechanism in the right valve of some representative ostracodes. A. *Craspedobolbina* (*Mitrobeyrichia*) *clavata* (KOLMODIN), No. G 271. B. *Beyrichia* (*Beyrichia*) *dactyloscopica* (MARTINSSON), No. G 272. C. *Calcaribeyrichia simplicior* n.sp., No. G 273. D. *Hammariella pulchrivelata* n.sp., No. G 274. (A. Subfamily *craspedobolbininae*, B–C. *Beyrichiinae*, C. *Amphitoxotidinae*.) A–D × 50.

In the *Craspedobolbininae* the fine ridge in the groove of the right valve is developed along its entire length (Fig. 17), but there is a clear tendency for the more dorsal of the two grooves of the second order to be suppressed, and the dividing ridge may be missing in the middle part of the hinge. This tendency is still more pronounced in the *Beyrichiinae* where only very narrow remains of the dorsal groove are found above the completely dominating ventral groove (Fig. 17). The ridge of the left valve has followed the development of the groove, is somewhat thickened towards the ends, and ends at the cardinal corners in incisions like those on the right valves. In *Amphitoxotidinae*, the material investigated has only one main groove in the right valve, corresponding to a ridge in the left valve (Fig. 17).

The ligament must have occupied very little space along the actual contact of the ridge and groove elements which articulate well with each other.

It is probable that the arrangement with the two subequal grooves and corresponding ridges is the more primitive. Unfortunately we cannot attain the information on the details in the attachment of the palaeocope ligament which would have helped us to discern whether the duplicate arrangements of the grooves and, partly, the ridges should be explained from mainly mechanical or mainly phylogenetic points of view.

As the hinge has no further influence on the problems discussed here, it will not be discussed in connection with the treatment of the different groups described. In the zygobolbine genus *Noviportia* it is essentially of the same type as in the *Beyrichiinae*. Illustrative material of the other subfamilies treated here has not been available.

Contact Margin.—A generalized section through the ventral part of the contact margin of a primitive beyrichiid is seen in Fig. 20. The solid free edges of the valves are set off as two shelves overlapping in a rabbet-like way. These extensions from the margin lie outside the marginal structures and seem to be missing in many palaeocopes, a fact which has led to the designation *extramarginal shelves* (Martinsson 1955, p. 7). The *overlap* conditions in the carapace, as illustrated by, e.g., *Craspedobolbina*, are then the following: Up to the more or less pronounced incisions inside the cardinal corners of the left valve the extramarginal shelf of this valve covers the corresponding shelf of the right valve. The shelf of the left valve, however, is overlapped again by a *covering marginal structure* (see below, p. 74) which is developed only on the right valve. In the hinge, however, it is the right valve which essentially covers the left one, according to the way of interpretation introduced above.

Outline

The lateral *outline* (Kesling 1951, p. 111, cf. Martinsson 1955, p. 7) of the beyrichiids is mostly distinctly *preplete* (Jaanusson 1957, p. 186), i.e. the greatest height of the carapace lies in front of the midlength. In some cases an almost *amplete* outline is found, as in tecnomorphs of *Noviportia* and certain *Beyrichia* spp. (the term *subamplete* will be used in less distinct cases). There can be slight variations in the degree of prepletion even within the same species, as, figuratively speaking, the unstable curved part of the outline is suspended in the rigid hingeline. A slight distortion of fossilized valves and carapaces, leading to stronger prepletion, is so common in certain samples that most measurements of the total length of the animal would be erroneous.

Lobation

Sulci.—The most conservative of the lobal features is the *adductorial sulcus* (Fig. 15), mostly situated at midlength of the valve, often somewhat in front of the midlength and very seldom (*Barymetopon*) inconsiderably behind it.

In some forms it communicates with the prenodal sulcus around the preadductorial node; in other cases it only forms a shallow pit curving around the site of this node (e.g., *Hamulinavis*, *Retisacculus*). In *Noviportia*, *Phlyctiscapha*, *Dolichoscapha*, *Apatobolbina*, and *Leptobolbina* it is entirely missing, its site being marked only by a *muscle spot* (in the genus *Bolbineossia* there is a very small, rounded pit), corresponding to the insertion of an undifferentiated muscle bundle on the inner side of the valve. In sulcate forms a spot or scar marking this muscle insertion can be seen distinctly only in *Neobeyrichia tuberculata*.

In front of the preadductorial node (knob, lobe) there is mostly a *prenodal sulcus* (Fig. 15). It is very often obsolete.

It is doubtful whether any more sulcal features homologous with sulci in other palaeocopes occur in the *Beyrichiidae*. The syllobial groove (Fig. 15; the "fissus" of HENNINGSMOEN 1954, Fig. 1, p. 19) is obviously not to be explained as a lobal feature (cf. below).

The lobes may be secondarily split up into a number of *lobules* (*lobuli*), separated by shallow *sulcules* (*sulculi*) according to the main pattern illustrated in Fig. 15.

PREADDUCTORIAL NODE, KNOB, OR LOBE.—This feature is almost as constant as the adductorial sulcus, absent only in *Noviportia*, *Phlyctiscapha*, *Apatobolbina*, *Leptobolbina*, and *Bolbineossia*, representing three different subfamilies. It can be completely isolated, connected with the syllobium by the *zygal arch* (Fig. 15, cf. HENNINGSMOEN 1954, p. 20), or almost assimilated with the anterior lobe by the obsoletion of the prenodal sulcus.

ANTERIOR LOBE.—There is never more than one primary lobe in front of the preadductorial node. In the *Craspedobolbininae* an *anteroventral lobule* can be separated from it by a shallow sulcule (Fig. 15). The anterior lobe can protrude over the hingeline with one *cusp*.

SYLLOBIUM.—There is never more than one lobal feature behind the adductorial sulcus, viz. the characteristic broad *syllobium*. Only in some *Amphitoxotidinae* does it become almost as narrow as the two other elementary lobal features. In a number of other palaeocope families it is corresponded to by two lobes separated by a third main sulcus (cf. below, p. 70). It is also very probable that it has been formed by the fusion of these two lobes, but there is never any trace of the sulcus. However, in the *Beyrichiinae* the syllobium protrudes over the hinge with *two cusps* which might reflect primitive conditions. The posterior of these cusps (the "outer horn" of HENNINGSMOEN 1954) can be almost or entirely obsolete which is normal in the other subfamilies. For the sake of consistency, the term "cusp" is used in the *Craspedobolbininae* for not very pointed structures; a common development of the dorsal part of the syllobium is then termed a *cuspidal plica*.

The syllobium has a more or less distinct furrow posteroventrally, the *syllobial groove*. As pointed out by HENNINGSMOEN (1954, p. 19) one of its edges

can form a swollen, lip-like feature which can be even more prominent than the groove itself. This is here termed the *callus* and may occupy either the upper or—rarely—the lower edge of the groove.

It is very doubtful whether the syllobial groove marks the site of an obsolete sulcus; if that were the case, the posterior syllobial cusp could not be a rudiment of an obsolete lobe, as the groove would cut almost straight across this lobe. It may have some significance, however, that the groove and its callus ridges have about the same site and orientation as the lower limit of the zygal crista or its continuation.

In the tecnomorphs of some genera the lobule below the groove is connected directly with the lower part of the anterior lobe and forms a *lateroventral lobe.*

In the *Beyrichiinae* the syllobium is sometimes secondarily subdivided into smaller elements. It has been found practical to introduce the terms *uncular* and *calcarine* lobules for two of them which are provided with major spines (Fig. 15).

Cruminal Lobation.—The formation of the beyrichiid crumina, which is originally a velar element, implies the assimilation of considerable parts of the lobes. In the *Craspedobolbininae*, *Amphitoxotidinae*, and *Beyrichiinae* this assimilation generally comprises large parts of the anteroventral lobe and results in the extinction of the zygal arch. In forms with a lateroventral lobe a displaced rudiment of this lobe is often found above the crumina.

In the *Treposellinae*, however, the crumina invades large parts of the syllobial space. All transitions are found, from a rather moderate occupation of the syllobium by a still mainly anteroventral crumina in the lobated *Strepula* to a strongly swollen syllobium with a gentle transition into the other parts of an unlobated carapace as in *Phlyctiscapha.*

Anteroventral Depression.—This feature (cf. Henningsmoen 1954, p. 19) is a shallow depression or even a distinct pit which is to be found in the tecnomorphs of most *Amphitoxotidinae* and many *Beyrichiinae* and can be traced in some *Craspedobolbininae.* It is situated in the same anteroventral position as the crumina in the females of the same species and is in its typical development connected with a pronounced thinning of the carapace.

Adventral structures

The *adventral structures* were defined by Jaanusson (1957, p. 188) in connection with a reconsideration of the ridge-, flange-, or frill-like extensions of the carapace as the basis for systematics largely based on the sexual dimorphism exhibited by some of these structures. He regarded them as ornamental extensions of the valve and distinguished between the velar, histial, and carinal structures. In the present paper the histial structure, characteristic of the hollinaceans, is left out of consideration, and the carinal structures are still regarded as ornamental and need not necessarily have an "adventral"

Fig. 18. A female (top, A) and a male (bottom, B) specimen of *Craspedobolbina* (*Mitrobeyrichia*) *clavata* (KOLMODIN), figured in oblique ventral view, × 50, showing the morphology of the adventral structures. Cf. Fig. 19; an explanatory cross-section is found in Fig. 20. Nos. G 275 (top) and G 276 (bottom).

position. The *velar* and the *marginal structures*, very similar morphologically and obviously of very similar morphogenetic origin, are united in a category of the same rank as the lobal and ornamental structures.

The occurrence of these structures throughout the palaeocope system, their morphology, and their scientific history were studied and summarized by JAANUSSON (op. cit., p. 191 sqq.). The structures were figured and the velar structure was used as a main classificatory feature by HENNINGSMOEN (1955, not in Text-fig. 1b where the designations have been confused).

Some linguistic remarks must be made as to the differences in the usage of terms connected with these structures.

In several branches of micropaleontology terms of the type *porate* ("provided with a pore"), *colpate* ("provided with a furrow"), *tuberculate* ("provided with tubercles"), etc. are used as descriptive terms. A similarly constructed term, *velate*, based on SCHMIDT's (1941) term *velum*, has found wide and indiscriminate applications and is, then, also used in connections such as "velate dimorphism", "velate ridge", etc. This is not entirely foreign to English usage—nor to scientific Latin—where words like "oval" and "ovate" are treated quite synonymously (though in this case the verbal construction "shaped like ..." is possible). However, the ending used in this case is derived from the Latin suffix *-atus* which is, both formally and logically, identical with the past participle ending of a (transitive) verb to be translated "provided with ..." etc. Neither the dimorphism nor the ridge is provided with a velum, and in this case the form *velar* (with an ending derived from the Latin adjective suffix *-alis*, *-aris*) should be chosen. The same is the case with the term "extra-lobate area" which does not signify "an area with an extra lobe" but "an area outside the lobation".

The problem becomes acute in any translation into other languages. Already in the Romance languages there is a logical need to distinguish, *e.g.*, between *dolonal* (Fr.) *dolonal* (Sp.), and *dolonale* (It.) when referring to the space enclosed by the dolon, and *dolonée*, *dolonada*, and *dolonata* when referring to the valve provided with a dolon. German and the Nordic languages generally adopt the Latin suffixes in terminological language (*dolonal*, *dolonat*, but the illogical examples can easily be demonstrated if one tries to use *dolonisch* and *doloniert* in German or *dolonisk* and *dolonerad* in Swedish without discrimination.

The velar and marginal structures in the beyrichiids are both primarily constituted by a great number of *tubules* standing close to each other and forming a structure which is strikingly frill-like when seen in lateral view. The lumen in the tubules in the velar as well as in the marginal structure is easily observed when the structure is broken (cf., e.g., Figs. 19, 33, and 100B). They were formed in an initial stage of the calcification of the carapace by a morphological or physiological differentiation of the epithelium. If the epithelium was differentiated morphologically the processes corresponding to the tubules must have been retracted or resorbed before the calcification was completed; There is never any communication of the tubules with the domicilium of the carapace except in one case referred to below (p. 92) where the completion of the last moulting had been interrupted in an early stage. The normal velar tubule never has an external opening.

Fig. 19 A. Adventral structures in *Craspedobolbina* (*Mitrobeyrichia*) *clavata* (KOLMODIN), seen in ventral view. Anterior end towards the upper left. ×75. Explanatory cross-section in Fig. 20; in this species the torus forms a crest near the velar margin. No. G 277.

Fig. 19 B. Anterior portion of the vertical marginal frill in the same species. Left valve, anterior hinge corner seen. ×75. No. G 278.

Both structures can be strongly specialized in the different subfamilies.

VELUM.—In the *Craspedobolbininae* the velum has mostly very thick and short tubules and a pronounced thick edge (*Craspedobolbina*), but even in closely related forms it can vary between a primitive velum with narrow tubules and no differentiated edge structures (*Apatobolbina*) and a solid *velar ridge* without any externally visible tubules. In the *Treposellinae* this ridge-like velum

is normal, if present at all, but radial streaks, probably corresponding to tubules, can be observed on examination of *Strepula* and *Garniella* spp. in transmitted light. The normal type in the *Amphitoxotidinae* is a broad velum of narrow tubules, but cases with a velum like that of *Craspedobolbina* occur, as shown in the present material by *Sleia*. The velum in the *Zygobolbinae* is a more or less narrow, solid ridge. In the *Beyrichiinae* it is mostly a *velar bend*, often spinose, but in some forms it becomes ridge-like, probably secondarily, and in the aberrant genus *Bingeria* it can even form a ridge.

In broad vela with narrow tubules, belonging to different groups, the tubules often have a transversal pattern of minute furrows and ridges resulting in a finely wrinkled appearance of the velum which makes it still more suggestively frill-like (Figs. 76, 77, 110, 115, etc.).

In the *Amphitoxotidinae*, even if the velum is very broad, it can be restricted to a part of the stretch between the cardinal corners. It is then often sharply cut off at the ends and continued only as a velar bend, if it can be traced at all. The most extreme example treated here is the genus *Atterdagia* where the female velum forms a very restricted wing-like extension behind the crumina (Fig. 130). The dimorphic development of the velum is treated below.

Marginal Structures.—These structures have proved to be much more complicated than realized hitherto, and their broad morphological-systematical aspects can only be slightly touched upon in this paper (nor will the overlap conditions in each genus be analysed). Probably they will add even more to the knowledge of the palaeocope development than the details of the hingement.

The *Craspedobolbininae* are once more the best starting point for a description. In *Craspedobolbina* they consist of two *vertical frills* orientated in the sagittal plane of the animal along the contact margin. In this genus, however, they are not equally broad all along but are widened in two crescent-shaped arches anteriorly and posteriorly (Fig. 18). Medioventrally they are marked only as a row of minute tubercles, almost isolated from each other (Figs. 18 and 19). They are symmetrically developed in both valves (Fig. 20).

A morphologically very similar *covering frill* is developed along the margin of the right valve only. It is equally broad along all the ventral part of the carapace and covers the overlapping extramarginal shelf of the left valve, lying at right angles to the vertical frills.

These structures may, congruently with the velum, be developed as solid flanges, as in the *Treposellinae* and *Zygobolbinae* (Figs. 96, 135, and 136). On the other hand, they may often be dissolved in rows of isolated tubercles or spines as in many *Craspedobolbininae* (Fig. 79–81 and 84) and some *Amphitoxotidinae* (Figs. 98, 101, and 103). In the *Beyrichiinae* the covering frill is mostly very well developed, but the vertical frills are very low (Fig. 178). Sometimes there may be a row of *accessory tubercles* outside the vertical frills (Fig. 20).

Ontogenetically the marginal structures are the earlier developed of the

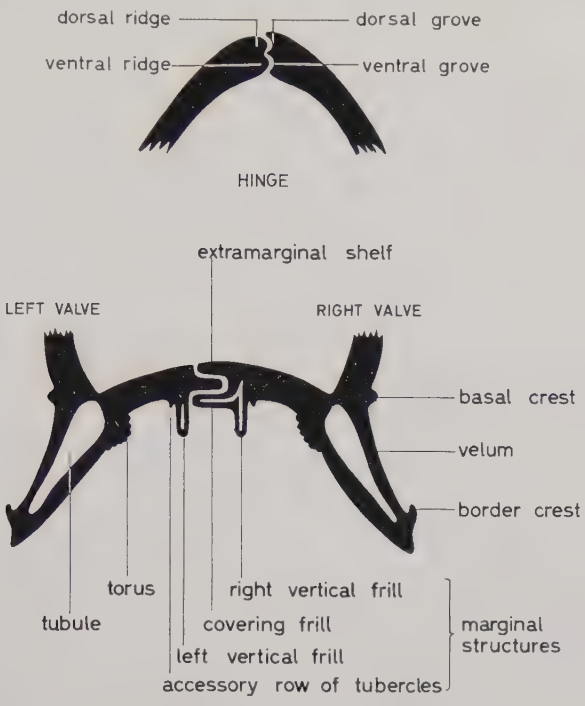


Fig. 20. Generalized cross-sections showing the contact conditions of the valves in more primitive *Beyrichiinae*. The luminar connection between the vertical and covering marginal frills of the right valve is not verified by investigations; the frills might well be independent of each other.
The sections can be used as a key to Figs. 18 and 19; however, the sections show a basal, striate toric swelling of *Apatobolbina* type instead of the toric ridge near the velar edge of *Craspedobolbina*. There is often a similar development of the torus and an ornamental ridge on the other side of the velum.

adventral structures. As shown by MARTINSSON (1956, Fig. 3) they are well developed even in the youngest carapaces and are then connected with the *acroidal processes* (cf. below, p. 77).

Ornamentation

GRANULATION, RETICULATION, AND PUNCTATION.—These three terms are sufficient for the description of the ground pattern in those beyrichiid carapaces which are not entirely smooth. *Granulation* (cf. Fig. 60) is by far the most common of these structures, occurring in most *Craspedobolbininae* and *Beyrichiinae* and in the *Zygobolbinae*. The normal pattern in the *Treposellinae* and *Amphitoxotidinae* is a *reticulation* (Figs. 94 and 105). In the *Craspedobolbininae* the reticulation is represented by *Bolbineossia* and *Dolichoscapha*. Reticulation of a special type is found in the beyrichiine genus *Bingeria* and its closest relatives.

All three terms are firmly rooted in traditional usage. The term *punctation* is used when the lumina in the meshes occupy less space than the walls between them, and the ornamentation has lost its network structure. This term has only few applications in species treated here, e.g. in *Aitilia* and locally in the treposellines; the *Kloedeniinae*, however, are typically punctate.

These structures may seem very different, but uncompleted investigations of valve surfaces, thin sections, and cleaned or fluoridized valves in transmitted light suggest that they might be very similar in origin. The granulation sometimes proves to consist of densely packed, very small rods. When broken they prove to have a lumen. The lumen may be much enlarged and a structure like that figured by Adamczak in *Kozlowskiella* (1958, Figs. 5 and 16; cf. also Kesling 1957a) is obtained. The primitiopsids show the same development of the reticulation. As far as the beyrichiid species treated here are concerned it seems evident that the cases of punctation are extremes of the common reticulation.

Verrucosity, Tuberculation, and Spinosity.—Superimposed on the granulation and, rarely, on the reticulation is a pattern of the second order. These structures are all homologous. For practical use the term *verrucae* is used for excrescences in the granulate surface shaped like a blunt wart or a obtuse cone without any distinct lateral limitation, *tubercles* for higher structures sharply set off laterally and *spines* when the cones are definitely acute as preserved in the fossil state.

The most primitive structures of this kind are enlarged granules spread out over the granulate surface of some *Craspedobolbina* species (Figs. 13, 54, 55, 60, etc.). Both in the *Craspedobolbinae* (e.g. Fig. 69, 63, 62, and 61) and in the *Beyrichiinae* (e.g. 173, 171, and 175) there is a series of transitional types of verrucosity. The typical tuberculate or spinose surface is found among the *Beyrichiinae* where there is often a clear differentiation of the tubercles or spines fields or rows. There are, then, a *velar* and a *supravelar row of tubercles or spines*. Some individual spines can also be distinguished, viz. the *calcarine spine*, situated below the adductorial sulcus on the lower anterior part of the syllobium, behind the crumina, the *uncular spine* situated on the hook-shaped lobule posteroventrally, and the *acroidal spine* in a position similar to that of the posterior acroidal process in other forms (Fig. 15).

If the calcarine spine is homologous with similar processes occurring in similar positions in three other subfamilies, as seems to be the case, this is one of the most persistent features in the beyrichiid carapace. In the *Craspedobolbininae* the process is assimilated with the velum which makes a slight bend towards it in tecnomorphs of *Hamulinavis*; in the females of these forms (Figs. 79–84) it is situated posteriorly on the crumina.

It is of some interest in this connection to reconsider how the outer chitinous layer might have covered the carapace. As suggested by Spjeldnaes (1951) for *Craspedobolbina clavata* ("*Beyrichia jonesi*") the pores contained in the

tubercles probably marked the sites of bristles or hairs. It is possible, too, that the chitinous layer in some cases lengthened spines ending with an open lumen as preserved in the fossils and that it played a relatively greater part in the probably incompletely calcified marginal structures. It is even possible that the surface granulation marks the existence of minute chitinous processes.

If the features mentioned were corresponded to by chitinous differentiations in this way it would also explain some peculiarities in the treposelline reticulation. The meshes sometimes prove to be narrower at the surface than deeper down in the carapace wall, thus forming rounded cavities with narrow openings. This is seen in KESLING's (1957 a) peels of *Hibbardia*, better in weathered material of *Kozlowskiella*, and better still in sections of *Primitiopsis* made subsequently to the recrystallized section published by MARTINSSON (1955, Fig. 5). In carefully prepared, well-preserved specimens of *Bolbiprimitia inaequalis* (Fig. 96, the adult male) the meshes prove to contain a central calcareous body. In *Aitilia* the females have a pronounced tendency to a punctation which is mostly entirely concealed under the fairly even granulation in the males; in this case there is a veritable dimorphism in the ornamentation.

It is probable, therefore, that the chitinous layer did not bulge into the meshes of the reticulation but covered them. It was lined with calcareous substance along the margins of the mesh cavities and sometimes contained a central calcareous body.

ACROIDAL PROCESSES.—Attention was drawn to the ontogenetic disappearance of these structures by MARTINSSON (1956, Fig. 3). As they are never present during the late ontogeny of the species investigated then, *Craspedobolbina clavata*, they were called larval processes. In the species referred to they occur only in the valve forming the overlap in the hinge, the right hand one. However, subsequent studies have shown that it occurs in adult specimens of several craspedobolbinines, even in *Craspedobolbina*, and in *Hamulinavis* they are, owing to different overlap conditions, found in the right valve, too. They are originally connected with the marginal structure; when a velum is developed the bases of the processes are fused with it. Acroidal processes occur in widely different parts of the palaeocope system, as in *Gravia*-like undescribed species from Gotland (cf. POLENOVA 1953, Pl. 1, fig. 1), *Coronakirkbya* (SOHN 1954, Pl. 5), etc. The homologization of these structures, however, including the acroidal spines treated above, still lacks a basis in a systematic survey and analysis of the very varied material extant.

CRISTAE AND CRISTAL LOOPS.—The term *carina* was introduced by HESSLAND (1949, Fig. 3d, ventral carina). It was drawn by KESLING (1951, Fig. 4) as a frilled structure above his frill (=velum). HENNINGSMOEN (1953) adopted the term according to HESSLAND's drawing (l.c.) and proved that it exhibited dimorphism. KESLING & COPELAND (1954) used the term for an ornamental structure in the kirkbyids. JAANUSSON (1957, p. 195) pointed to the fact that ever since its introduction the term had covered several different types of

structures –a homonymous term used in cytherids and cytherellids existed already before it was introduced in the palaeocopes (cf. VAN DEN BOLD 1946)— and coined a new term for the dimorphic structure, the histium.

He then suggested the term *carina* to be used "in a wide sense, including different kinds of non-dimorphic adventral ridges" (op. cit., p. 196) "situated lateroventrally and often occupying about the same position as the connecting lobe" (op. cit., p. 188).

Ridges of this kind in the position indicated are very common, in beyrichiids, bassleratiids, primitiopsids, kirkbyids, leperditellids, and others. But in many cases these structures belong to branched systems of ridges or crests which cannot be referred to as "adventral", are strictly non-functional, never tubulous but have a morphogenesis in common which never leads to homologies with tubulous, "frilled" structures. In this study it has been necessary to exclude them from the adventral closing and dimorphism-bearing structures as defined above. The term *crista* is used here—in so wide a sense that it includes both *carina* and *dorsal plica* sensu JAANUSSON—for these ornamental crest systems occurring in beyrichiids and other ostracodes, without respect to homology.

Attention should be drawn, however, to the very similar arrangement of the cristae in the *Beyrichiidae* and some other families.

In *Craspedobolbina* some species have a pattern of cristae, the most prominent of which is the *zygal crista* (Fig. 15), running across the preadductorial knob, continuing along the zygal arch, and bending upwards across the syllobium and disappearing behind the dorsal ridge of the syllobium. Along this ridge there is another crista of a similar kind, bent down along the posterior limit of the sulcus. A distinct crista is found on the cusp of the anterior lobe; in the tecnomorphs it is also found anteroventrally on the same lobe (Fig. 54). The lateral parts of the cristal system can be restricted exclusively to the preadductorial knob.

Such cristae also exist in *Strepula* (Fig. 90), *Piretella* (JAANUSSON 1957, Pl. V; SARV 1959, Pl. III), *Tallinnellina*, *Rigidella*, *Steusloffia* (JAANUSSON, op. cit., Figs. 35, 38, and 39) and others. So far they can be arranged in a quadripartite system with one crista on the preadductorial node, one in front of it, and two behind it, extending onto dorsal cusps or ridges. In other forms they are further branched (*Pseudostrepula*) or existing mainly as a curved ridge around the sulcus, connected with dorsal cristae (*Hesperidella*).

In *Gannibeyrichia* (Fig. 193) and *Navibeyrichia* (Figs. 196B and F) there are also crista-like structures of another category covered by the definition of the *carina* but certainly not to be regarded as adventral structures if these are distinguished from the ornamental structures. Furthermore, there are cristae on the crumina of many *Treposellinae*.

A special category is represented by the *cristal loops* in some *Amphitoxotidinae* (Figs. 120–123) and *Hexophthalmoides* (Figs. 202 and 203).

ORNAMENTATION OF THE VELUM.—Apart from the tubulosity and the fine

transversal wrinkled pattern there are still some ornamental structures associated with the velum and the subvelar field. A *border crest*, consisting of fine denticles, about half as broad as the tubules in the velum, is present in some *Amphitoxotidinae* (Figs. 20 and 105, cf. p. 222). In most *Craspedobolbininae*, *Amphitoxotidinae*, and *Beyrichiinae* there is a structure, generally shaped as an often striate, low to ridge-like swelling along the velum or the subvelar field. This *torus* or *toric structure* is an important diagnostic character, especially in the *Amphitoxotidinae*. In *Berolinella* and associated genera it forms a more pronounced ridge or crest, corresponded to by a *basal crest* (Fig. 20) on the other side of the base of the velum. For the present the term is introduced with no claims as to homology.

Ontogeny

Preadult moult stages and growth

The following sections will summarize, without a complete repetition of the previous discussion, but in the light of new results in connection with the present study and of recent publications, the results published in two preparatory studies to which reference is made (Martinsson 1955 and 1956). Special attention is drawn to two subsequent publications on beyrichiid ontogeny, by Kesling & Soronen (1957) and by Adamczak (1958).

The first study of beyrichids from an ontogenetic point of view was published by Verworn (1887) who derived a *Beyrichia* species from smooth forms belonging to another family, probably tecnomorphs of the primitiopsid genus *Amygdalella*. The first ontogenetic analysis based on biometric data from a homogeneous beyrichiid population was published by Spjeldnaes (1951), dealing with *Craspedobolbina clavata* from Mulde on Gotland.

A fossil ostracode fauna exceeds in polyformity by far the number of species. This is due to the presence of immature moult stages. Between widely different parts of the ontogeny of a species the morphological differences may be greater than between related species. It is important to know how the carapace changes during the ontogeny, how the adult characters are to be recognized, and in what part of the ontogeny they are first acquired. This information is essential as a basis for taxionomy and classification.

Craspedobolbina clavata passes through nine free moult stages (Spjeldnaes 1951, Martinsson 1956). Four *Kozlowskiella* species have the same number (Adamczak 1958). Kesling & Soronen (1957) report 6 stages in *Welleria*, but the number of specimens measured is not sufficient to prove that smaller stages did not exist. Among the primitiopsids six instars are known in *Primitiopsis* (Martinsson 1955). The hollinid *Ctenoloculina* has nine stages (Kesling 1952). The kirkbyacean *Ectodemites* has nine stages (Cooper 1945). These seem to be the only investigations of palaeocope growth series attaining or approaching completeness.

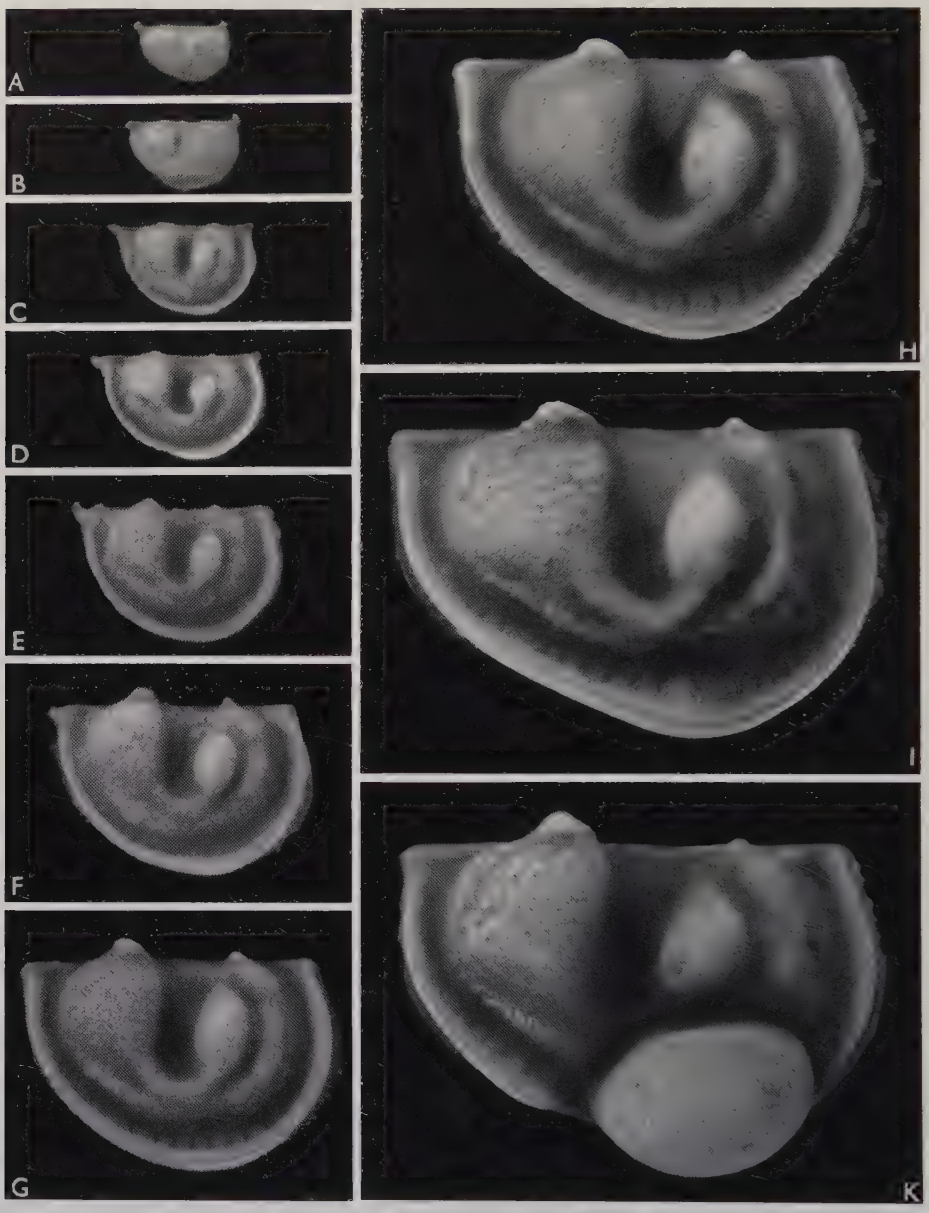


Fig. 21. Ontogeny of *Craspedobolbina* (*Mitrobeyrichia*) *clavata* (KOLMODIN) A. Stage 9 (No. G 279). B. Stage 8 (No. G 280). C. Stage 7 (No. G 281). D. Stage 6 (No. G 282). E. Stage 5 (No. G 283). F. Stage 4 (No. G 284). G. Stage 3 (No. G 285). H. Stage 2 (No. G 286). I. Stage 1, ♂ (No. G 287; note the enlarged anteroventral tubules). K. Stage 1 ♀ (No. G 288). A–K right valves, × 30.

SPJELDNAES (1951), however, asserts that *Craspedobolbina* moulted once or twice in the crumina and had two more instars existing only in the crumina. In the sections made in connection with the present study, there are no outlines of larvae in the cruminae which are smaller than the youngest free instar and at the same time can be proved not to cut the larval carapace strongly exsagittally, dorsally, ventrally, or obliquely transversally (cf. MARTINSSON 1956, p. 14). It is impossible to avoid regarding the existence of these moult stages as still unproved.

As long as we do not know the number of moult stages or still have reasons to expect that this number may vary, we have to number them in practical work starting with the last one, the adult. It is very rarely that we can be sure of having found the earliest moult stages.

Craspedobolbina clavata has been investigated more thoroughly than any other palaeocope ostracode in this respect (Figs. 21 and 22). It is illustrative as to the degree of the changes taking place during the ontogeny. They will be briefly reviewed in the following (cf. Fig. 21).

STAGE 9.—In the youngest stage the lobation consists of a very faint sulcal depression in the adductorial region and an equally faintly developed preadductorial node in front of it. The adventral structures consist of well developed marginal frills (MARTINSSON 1956, Fig. 3), in the right valve connected with the acroidal processes. Parallel and close to it there is, at least in most cases, a fine, callose line developed in the surface pattern, the orimentary velum. Elsewhere the granulation covers the carapace evenly. In this stage the acroidal processes are relatively longer than in subsequent stages; the anterior of them is generally bent upwards and backwards in a fairly sharp hook; the posterior one is straight, generally pointing slightly upwards so that its continuation bisects the posterior cardinal angle.

STAGE 8.—The lobal features in the preceding instar are slightly more pronounced and an addition in the very distinct syllobial groove is to be found. There is already a distinctly marked velar ridge. The granulation covers the entire carapace without differentiation. The acroidal processes are developed in the same way as in stage 9.

STAGE 7.—The lobation becomes still more distinct, and the prenodal sulcus is added. The velum is developed as a flange, somewhat extended anteroventrally. The granulation does not occupy a smooth zone along the velum, and the deeper part of the adductorial sulcus is also smooth. The anterior acroidal process is not hooked.

A slight displacement of the sulcus in towards the anterior and a gradual filling out of the postadductorial half of the carapace is observable even without the aid of measurements.

STAGE 6.—The zygal arch becomes distinct, uniting a distinct preadductorial knob with the syllobium just above the groove. There are small lobal cusps. The anterior extension of the velum can be so pronounced that it forms a bend in the outline. The tubulosity of the velum is discernible.

STAGE 5.—The lobal cusps are higher than in the preceding instar. The tubulosity of the velum is distinct, and there is a rounded, ridge-like swelling along the margin. There is seldom any trace of the anterior acroidal process.

STAGE 4.—The syllobial groove has during the course of the ontogenic development become relatively less distinct. There is still a short posterior acroidal process.

STAGE 3.—An orimentary verrucosity, connected with the existence of pores in the carapace, is discernible. There is a tendency towards fusion of the ornamentary granules

below the syllobial groove. A very small rudiment of the posterior acroidal process may be present.

Stage 2.—The verrucosity is distinct on the syllobium, below its callus and the zygal arch, and on the anterior lobe where the pattern stresses the faint separation of an anterior lobule. Already in this stage there may be a differentiation in the width of the velar tubules anteroventrally.

Stage 1.—In the males the velar outline becomes more sharply bent posteroventrally, and the velum is strongly flattened anteroventrally, sometimes in connection with the widening of one or more tubules. The verrucosity is very distinct, and the syllobial cusp has reached the height of its characteristic development. In the females large parts of the carapace and its lobal and adventral extensions have been metamorphosed in connection with the formation of a crumina (cf. the following main section).

Reference is made to Spjeldnaes's (1951) paper for minor differences in observation and major differences in interpretation. Metric growth data have been provided numerically by Spjeldnaes (op. cit., total length and height) and Martinsson (1956, hinge length and height over the adductorial sulcus). Graphically they are reprinted here in Fig. 22.

The increase in size between two moults of *Craspedobolbina clavata* takes place according to a linear growth factor not much deviating from the ideal 1.26, corresponding to a doubling in volume; similar conditions are well-known from a long series of investigations in different ostracode groups (for references, see Martinsson 1955 and 1956). Only the last moulting, as can be read directly from the dispersion diagram (Fig. 22), implies a somewhat smaller increase in length (mean growth factor 1.19 in the male and 1.18 in the female) and a considerably smaller increase in height of the slender male carapace (1.12), as is still more pronounced in the female (1.03). In the female this does not imply the corresponding decrease in the volume growth factor, as the cruminal metamorphosis has resulted in a displacement of the domicilial space and might have influenced the point of measurements (the specimens were measured, however, as if there were no constriction of the velum below the adductorial sulcus).

The ontogenetic differentiation of the marginal structures and of the ornamental structures of the subvelar field have not been investigated in detail.

Brood care

Hessland (1949, Pl. XIV, Fig. 9; p. 125) discovered two small larval specimens in a cruminate beyrichiid carapace—it can now be determined with certainty as a *Craspedobolbina*—which had never been open so that marl substance or fossil fragments could penetrate into it. Spjeldnaes (1951) sectioned about 60 cruminate specimens of *Craspedobolbina clavata* and found larvae in nearly half of them. Martinsson (1956) repeated the study with 34 sections and found larvae in 6 of them; in this connection it was checked in 53 sections that no larvae are found in specimens of the other sex. Cruminae of *Bolbiprimitia*

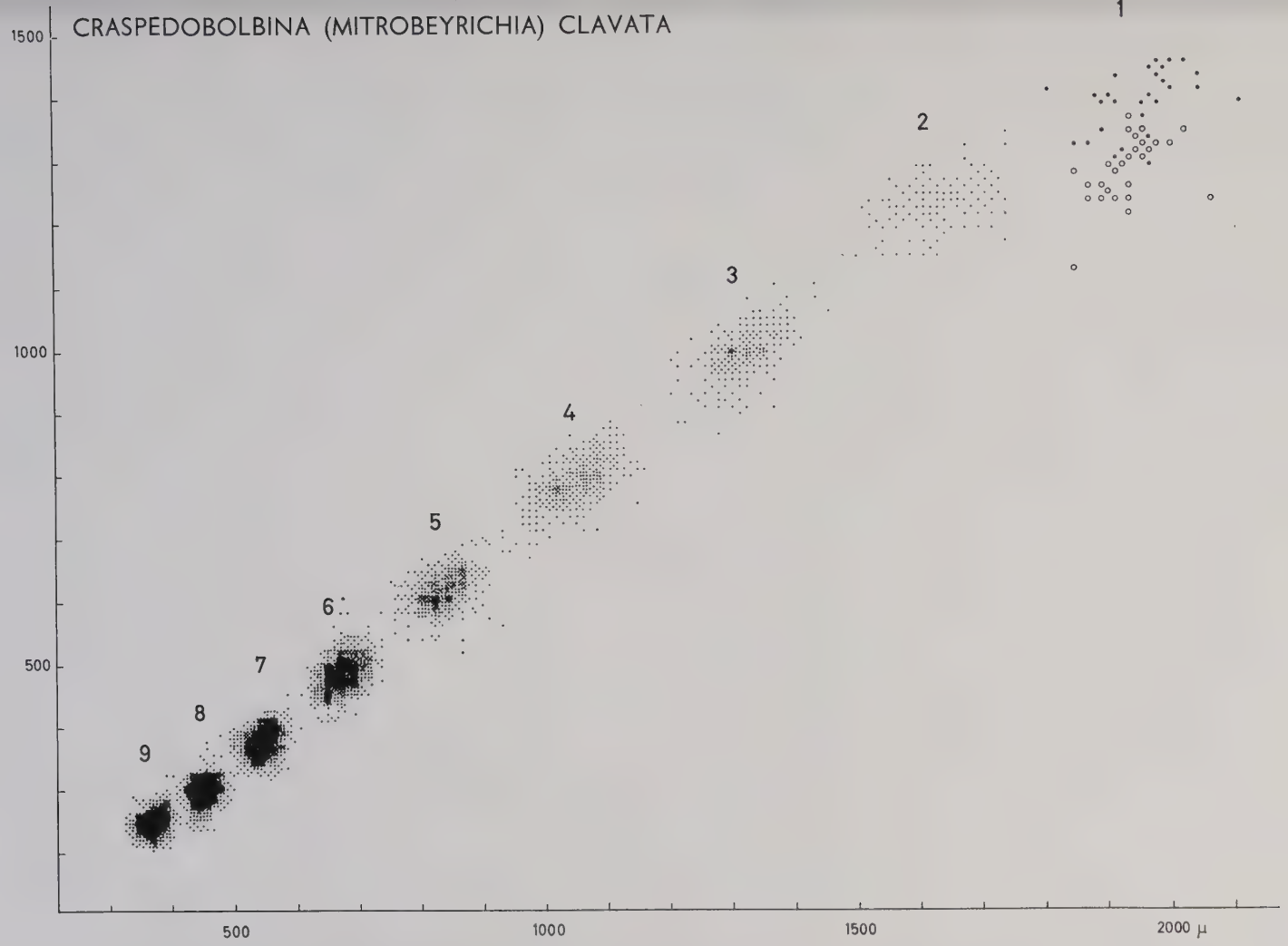


Fig. 22. Scatter diagram of hinge length (abscissa) and sulcal height (ordinate) in a sample (MS: 10: 1955: 1, representing 3461 specimens) of *Craspedobolbina* (*Mitrobeyrichia*) *clavata* (KOLMODIN), showing moult stages in this species. Material from Mulde.

inaequalis have also proved to contain larvae; in a female sectioned their number exceeds 9 at least.

It is, then, well established that small larvae were kept in the crumina, and it is probable that the eggs hatched in the same place. It must be regarded as insufficiently proved whether the larvae escaped immediately after hatching or whether they were kept there even long enough to moult twice as suggested by Spjeldnaes (op. cit.). This will be the subject of a special investigation based on serial sections.

Sex and sex ratio

Triebel (1941, p. 365) states that the sex ratio in beyrichiids is strongly in favour of the non-cruminate sex ("dass die höckertragenden Formen viel seltener sind als ihre Parallelformen", l.c.; Schmidt 1941, p. 12, makes similar statements) and believed that the cruminae were male characters caused by extraordinarily large spermatozoans like those in recent ostracode suborders. The brood care makes the latter part of the statement impossible, and a brood or egg care by male specimens is not known in nearer parts of the animal kingdom than the pantopods. Still, it has been proved only by analogy that cruminate heteromorphs and dolonate heteromorphs—among which parthenogenesis seems to be present—are females (Martinsson 1956).

Provided that *Clavofabella reticristata* is parthenogenetic (op. cit., p. 16)—and it is against all experience that the males should develop a dolon or that they should not be found together with the female specimens—the last link in the argumentation is available. As it is demonstrated below that the crumina developed from a dolonal structure, the parthenogenetic dolonate primitiopsid and the cruminate beyrichiids must both be females.

The sex ratio is not dominated by the males as suggested by the observations of previous authors. This misconception must be based on the fact that subadult tecnomorphs were included in the calculation. A calculation based on metric analysis of *Craspedobolbina clavata* gave the ratios 50:50 and 51:49, and a rather similar distribution of the sexes seems to be the normal in palaeocope ostracodes (Martinsson 1956, Table 3).

While there is no doubt as to the sex in beyrichiids, the term tecnomorph (Jaanusson 1957; cf. Martinsson 1956) still is a practical and necessary term for adult and preadult non-cruminate specimens. In this paper, though wrong from a strictly logical point of view, the word female is used for the heteromorphs, i.e. the adult females only.

Appearance of dimorphic characters

There is at present, in spite of thorough investigation, no beyrichiid known with completely developed dimorphic characters in a preadult moult stage.

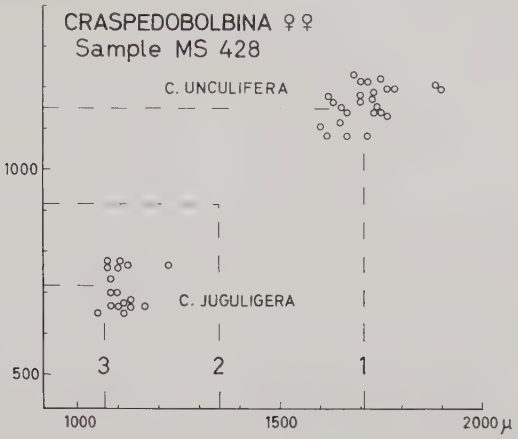


Fig. 23. Scatter diagram showing size dispersion of adult females of two sympatric *Craspedobolbina* species. Diagrams of this type, stating estimated growth rate (1.26) between the moult stages (dashed lines) have been used at the beginning of the investigation to control whether smaller females could be subadult stages of the larger ones; in the present case the cristae later found to be characteristic of *Craspedobolbina* (*Craspedobolbina*) were found to be absent in stage 2, and other species of the subgenus were found at other localities.

With very few exceptions there are no transitional forms between a tecnomorph and a normal cruminate female; the formation of the crumina was a metamorphosis taking place after the penultimate carapace was shed and before the ultimate carapace became calcified. The exceptional transitional forms occur extremely rarely, mostly corresponding in size to the adult female, in some cases, however, to the penultimate moult stage.

This statement gives a revised picture of the preadult dimorphism. As reviewed in a preparatory study (Martinsson 1956, pp. 10–13) cases referred to as preadult dimorphism occur in different species of several families. However, the two beyrichiids considered then can be excluded. *Beyrichia* cf. *jonesi* from the Upper Visby Beds, recorded by Spjeldnaes (1951) to have cruminate specimens of two different size groups, has been proved to include two new species, *Craspedobolbina unculifera* and *C. juguligera*. Similarly, some small forms included with hesitation into *Beyrichia dactyloscopica* by Martinsson (1956) have proved to belong to two new species, *B. peponulifera* and *B. morifera*. However, in the samples containing these three species there has been found, after the study of an enormous material, one single specimen smaller than a female of *B. morifera*, with an ornamentation which would be possible for a preadult stage of this species and with a completely developed but not well inflated crumina (Fig. 155 D; cf. p. 289).

Statements about the existence of a preadult dimorphism—an exceptional neoteny—obviously have to be made and treated with great caution unless they are based on measurements of a homogeneous population of a species possessing specific characters of such a quality that they cannot be expected to conceal another species differing only in size.

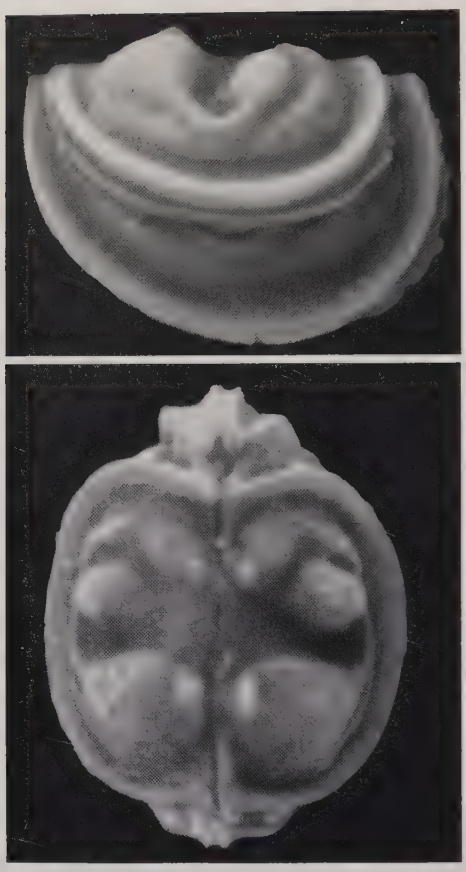


Fig. 24 A. Retention of moults in *Craspedobolbina* (*Mitrobeyrichia*) *clavata* (KOLMODIN). Young right tecnomorphic valves in lateral view. ×40. No. G 289.

Fig. 24 B. Same phenomenon. Dorsal view of tecnomorphic carapace; anterior end up. ×40. No. G 290. In entire carapaces like this one, the preadductorial knobs of the new carapace are suggestive of keeping the old carapace in place. As shown by Fig. 24 A, however, single valves are retained even if the new valves are separated, and there are also single retained valves on entire carapaces.

Moulting and retention of moults

No method has been found which allows a general distinction between exuviae and dead specimens. No resorption or age phenomena occur in those exceptional cases in which we know that carapaces or valves are exuviae, i.e. when they have been retained by the following instar (Fig. 24, cf. COOPER 1945, Pl. 57).

These rare specimens are as a rule represented by entire carapaces, and it is probable that many of the normal carapaces are exuviae, too.

The mechanism of this abnormal retention is difficult to reconstruct. It is possible that the carapaces were united along the hinge-line, but by chance the anteroventral margin of the shed carapace reaches just over the preadductorial knob of the new one which might have contributed to the retention.

The cases of retention allow a calculation of growth rates between moult stages of the same specimen. Some examples of the increase in hinge length are given below. Only *Craspedobolbina clavata* has been considered.

Retained exuviae	*New carapace*	*Moult stages*	*Growth rate*
899 μ	1.085 μ	5–4	1.21
1.131 μ	1.340 μ	4–3	1.18
1.085 μ	1.351 μ	4–3	1.25
1.098 μ	1.331 μ	4–3	1.21
1.085 μ	1.358 μ	4–3	1.25
1.078 μ	1.364 μ	4–3	1.27
1.131 μ	1.331 μ	4–3	1.18
1.438 μ	1.744 μ	3–2	1.21
1.697 μ	1.997 μ	2–1	1.18
1.730 μ	2.063 μ	2–1	1.19

The values are obtained from different moultings; the growth rate is in all cases but one lower than 1.26 and also lower than values obtained as means or medians in populations of the same species (MARTINSSON 1956, Table 2). No adult female has been found with a retained tecnomorph of stage 2.

Dimorphism and cruminal metamorphosis

Dimorphism in palaeocope ostracodes

An historical review of the palaeocope dimorphism and its bearings on classification was published by JAANUSSON (1957, pp. 197–226). SWARTZ's (1936) and HENNINGSMOEN's (1953) systems are referred to as the main steps towards the system proposed in JAANUSSON's paper, consistently built up on the existing knowledge of the dimorphism and the adventral structures exhibiting the dimorphic characters. The tenability of these classificatory principles has been further strengthened by subsequent findings.

However, this development has not only consisted in an accumulation of new observations and data on dimorphism, but it has also resulted in new genetical and taxionomical aspects of the different types of dimorphism. As an introduction to the following discussion some of these aspects must be reviewed. As the inclusion of the *Kloedenellacea* within the *Palaeocopa* is untenable (cf. p. 127), the type of dimorphism found in this family is not considered.

VELAR DIMORPHISM.—A basic type of dimorphism is developed by the velar structure. It is displayed by the specialized development of a part of the female velar structure, the *dolon*. The specialization typically consists of a broadening of the velum anteroventrally. If different lines of homology are followed, cases with a markedly anterior dolon are met with; the dolon may be extended along a considerable part of the velum and may be more or less convex; in an advanced genus, *Chilobolbina*, it forms a closed anteroventral pouch. In a specialized, but possibly phyletically heterogeneous family, the *Primitiopsidae*, there is a posterior dolon, developing a closed pouch in four not very closely related genera (MARTINSSON 1960a). There is sometimes a radial stria-

tion of the velum; as shown in *Chilobolbina* it is homologous with the *tubulosity* of the velum in the following group. A solid flange or ridge seems, however, to be a primary type of velar structure in this group.

Cruminal Dimorphism.—This type of dimorphism, known only from the *Beyrichiacea*, has been distinguished as a domiciliar type of dimorphism in contrast to the extradomiciliar velar and histial types. However, its main characteristics, pouches or swellings incorporating different parts of the carapace wall and forming direct protuberances of the domicilial space, can be derived both ontogenetically and phylogenetically from an anteroventral *dolonoid* extension of a velum. In this type of dimorphism it is possible that the *tubulosity* of the velum is a primary feature; it is evident that a tubulous velum can be reduced to a ridge or even disappear. The documentation behind these statements will be the theme for the major part of this section.

Histial Dimorphism.—According to Henningsmoen (1953) and Jaanusson (1957) the inner of two parallel adventral flanges in a group of primitive *Hollinacea* is identical with the velum in other superfamilies. The outer flange was termed *histium* by Jaanusson (op. cit.). If the established lines of homology are followed, it is found that the histium develops a *dolon* very similar to that formed by the velum. In a few cases the dolon exhibits the same kind of *tubulosity* as the velum. It is unknown whether the hollinacean velum can also develop a dolon of the common type; the dimorphism may, however, be manifest in the absence of both structures in the tecnomorphs. The very specialized *locular* type of dimorphism, with a series of hollows opening towards the subhistial field of the female, is exclusively connected with the histial structure.

Common Features in Palaeocope Dimorphism.—*Palaeocope dimorphism is always manifested by, or associated with, the formation of a dolon by an adventral, often tubulous, structure.* As far as we know at present the evidence behind this statement is distributed on two systems of homologies, one for the velar and cruminal, another for the histial type of dimorphism. The most important key problem in palaeocope morphology and systematics is at present to clarify the analogies or homologies between these two systems. Interest is then primarily directed towards the genera with both velum and histium, such as *Carinobolbina*, *Sigmoopsis* and *Sigmobolbina*, for verification of the velar nature of the subhistial structure. An examination of the material behind Jaanusson's (op. cit.) distinction of the histial dimorphism strikingly supports this homo-

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Fig. 25 (opposite page). *Craspedobolbina* (*Mitrobeyrichia*) *clavata* (Kolmodin). Adult specimens from the Mulde Beds at Mulde (reproduced from Martinsson 1960 b, Pl. I). 25:1. Male carapace, ventral view (anterior end up), showing velum with edge, torus, and tubules. The marginal structures are divided into an anterior and posterior crescent-shaped portion on each valve; the covering structure is seen between them. No. G 213. 25:2 Female carapace (same orientation) with fully developed crumina, showing the contraction of the velum and the dolonoid scar and the persistent ridge on the crumina. No. G 214. 25:3. Same details, seen in internal view of a right valve (anterior end to the right, ventral side up). Distal parts of the marginal frills broken away. No. G 215. All ×45.

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logy. Then, however, we are faced with a curious case of far-reaching homoeomorphy, with two adventral structures both forming a dolon which may even, in the oepikiid line, show extreme similarity in morphological details. The examination gives some support to a third approach to the problem, viz. that both flanges, though present side by side, might have a common genetic origin which could explain both the dolonal and the locular dimorphism in the hollinaceans. The problem, however, has no consequences which touch the beyrichiid dimorphism to any great extent.

Male characters in the *Beyrichiidae*

In those species investigated in this respect the last moulting results in a carapace without any new morphological differentiations as compared with the younger tecnomorphs. In *Craspedobolbina clavata* the carapace is relatively somewhat lower. The posteroventral bend of the outline becomes markedly sharper. There is a tendency to formation of one or a few wider tubules in the anteroventral part of the velum. Lobation and ornamentation follow up trends which have developed gradually in earlier tecnomorphic stages.

Origin and metamorphosis of the beyrichiid crumina

Intermediary dolonoid stages

Normal Conditions in the Craspedobolbininae.—As stressed in the preceding chapter there is normally no documentation in fossils showing the course of the metamorphosis taking place during that moulting which starts with the shedding of the last female tecnomorphic carapace. The differences in the adventral morphology of a male and a metamorphosed female carapaces can be studied in Figs. 25: 1 and 25: 2.

The details in the ventral morphology of a normal crumina can be easily identified in Fig. 25: 3. They consist of a narrow, slightly curved furrow just outside the marginal structure. A little farther from the margin, subparallel to, and slightly longer than, the furrow, there is a ridge which is missing in several craspedobolbinine genera. This ridge is not the edge of the velum, nor a toric structure.

Fig. 26 (opposite page, reproduced from Martinsson 1960 b, Pl. II). 26: 1–3. *Craspedobolbina* (*Mitrobeyrichia*) *clavata* Kolmodin. Fragmentary right valve with cruminal metamorphosis interrupted in a dolonoid stage. Lateral view (1) showing failing incorporation of the zygal ridge and other wall elements, oblique ventral view (2, anterior end towards the upper right corner) showing the development of the closing flap and the persistent ridge, and internal view (3) showing the tubules of the dolonoid wall in the closing stage, before the appearance of the secondary opening. No. G 216. ×45. 26: 4–6 *Craspedobolbina* (*Mitrobeyrichia*) *variolata* n.sp. A male valve (4, No. G 204), a valve with a dolonoid pouch in an early stage of development (5, No. G 205), and a completely developed female valve (6, No. G 206). ×30.

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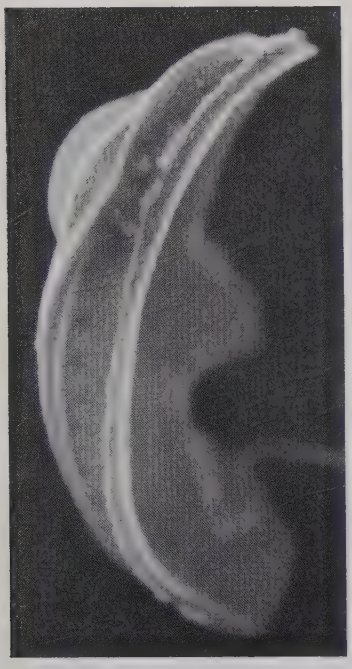

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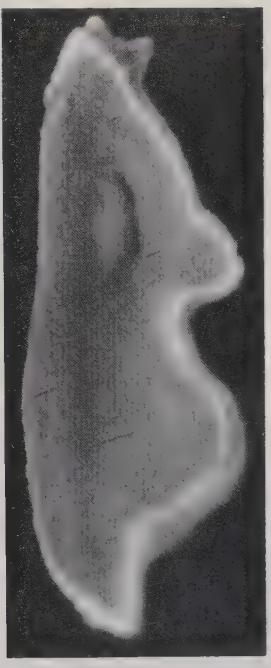

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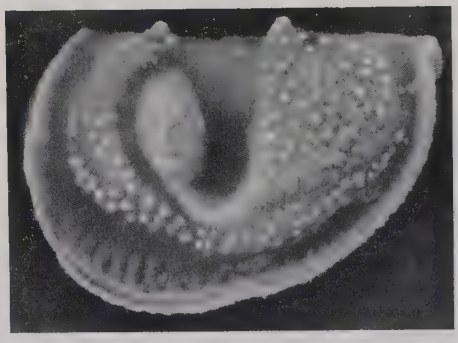

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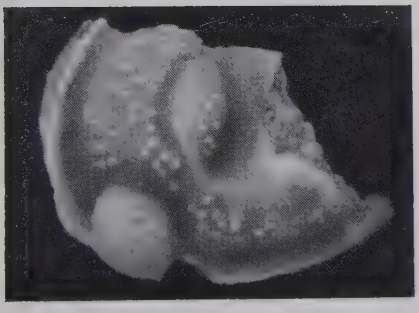

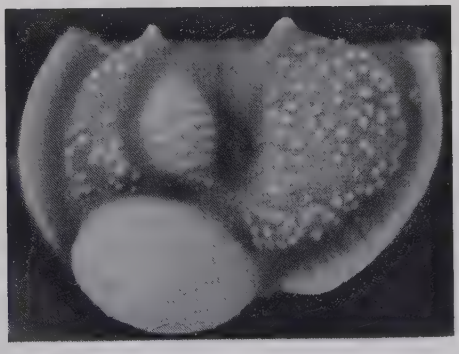

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As will be enlarged upon later, the furrow is the remainder of a circular opening, and the area between the furrow and the ridge is the proximal part of a triangular flap of the velum which has been introduced into the opening and has been pressed against the admarginal part of its edge. These conditions are shown more illustratively in another *Craspedobolbina* species (Fig. 42: 4).

The Earliest Stage.—The earliest dolonoid stage is shown in Fig. 28. A small bulge is developed on the outside of the anteroventral part of the velum. Corresponding to it on the inside is a cavity which is considerably less pronounced than the exterior bulge mentioned. The edge of the velum and the ornamental ridge along its outside have become sharpened, and this part of the velum already forms a very obtusely triangular flap. The toric ridge inside the velar edge forms in this specimen a small pit between the cavity and the edge.

The inside of the valve shows conditions which represent a stage which was unknown when a preliminary report on these questions was published (Martinsson 1960b). This is the only beyrichiid valve found in the entire material where the normal tubules open towards the domicilium. The dolonoid pouch consists of three such tubules, the central of which is flattened and considerably enlarged. The partitions separating this tubule from the adjoining ones are still well developed, and their attachment to the walls of the main velar fold can be observed on immersion of the specimen, but they have been stretched by the expansion of the central tubule so that there is not much lumen left in the adjoining tubules.

At this stage obviously the epithelium of the hypodermal fold formed a series of processes into the lumina of the tubuli. The hypodermis began to project into an anteroventral tubule in a somewhat larger process or lobe. In this valve the calcification must then have taken place without a retraction or resorption of any epithelial processes.

This statement has far-reaching consequences but is based on only one specimen. Its state of preservation and observations during the preparation are further commented below. A few other specimens have dolonoid pouches which are in the same primitive stage of development (Fig. 29), but as far as the interior of these specimens could be examined the tubuli proved to be closed.

The Typical Dolonoid Pouch.—In most cases of an incomplete metamor-

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Fig. 27 (opposite page, reproduced from Martinsson 1960 b, Pl. III). 27: 1–3. The same specimen of *Craspedobolbina* (*Mitrobeyrichia*) *variolata* n.sp. as in Fig. 26: 5 (No. G 205), seen in ventral view in different inclinations and light angles (anterior end in all figures towards their upper margins, source of light in conventional position). 27: 4–8. *Craspedobolbina* (*Clavobolbina*) *acuminulata* n.sp. Left valve in lateral and internal views, with cruminal metamorphosis interrupted in a dolonoid stage (4–5, No. G 217), lateral and ventral views of another left valve in which the metamorphosis has evidently failed owing to damage to the anteroventral region of the carapace wall involved (6–7, No. G 218), and a normal left female valve (8, No. G 219) in lateral view. 27: 1–3 × 45, 27: 4–8 × 30.

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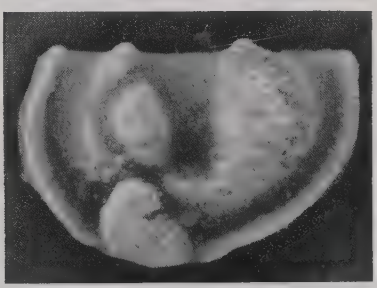

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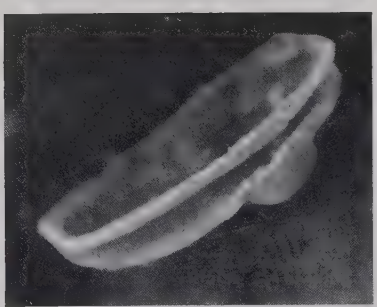

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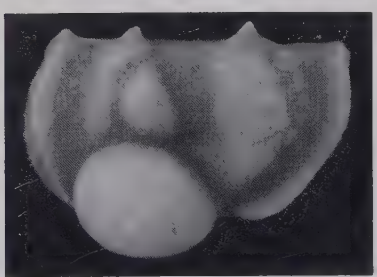

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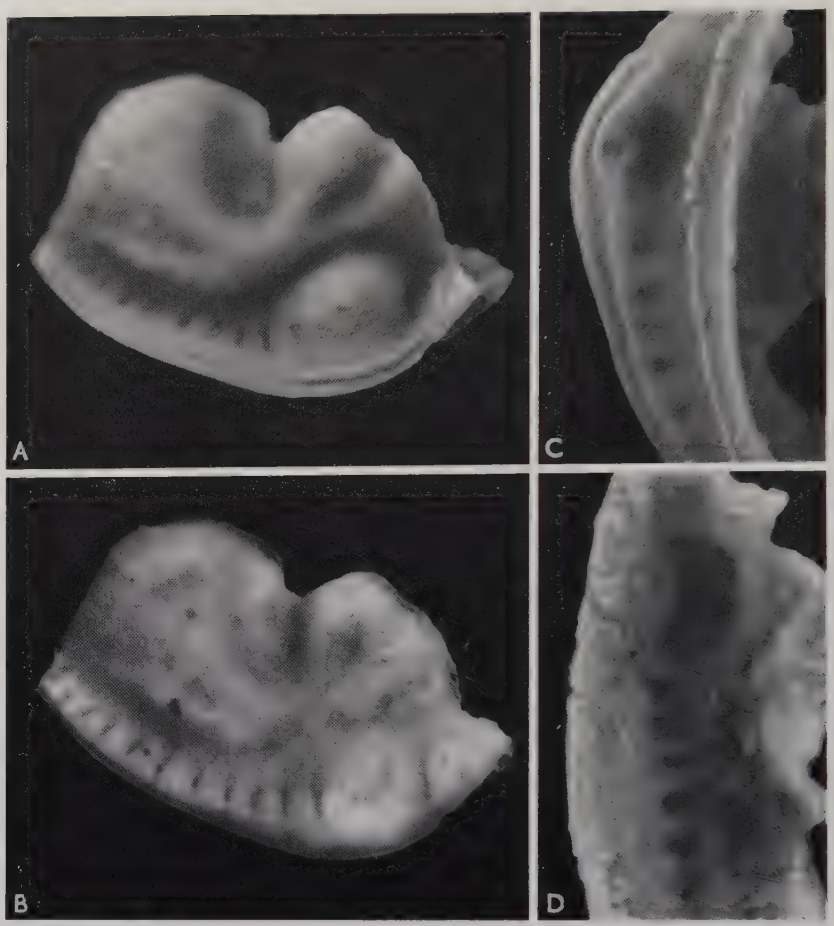


Fig. 28. A fragment of a right valve of *Craspedobolbina* (*Mitrobeyrichia*) *clavata* (KOLMODIN) with the earliest stage of the cruminal morphosis found (No. G 243). A. Lateral view, incident light. B. Lateral view, alcohol immersion, incident light, showing the partitions between the tubuli of the velum. Between the two normally distinct partitions (even the tubule limited anteriorly by the posterior of these tubules has been to some extent engaged in the formation of the crumina) there are two narrower lines marking the lateral attachment of the partitions pushed aside and thinned out by the invasion of the central tubule. C. Ventral view, showing the shallow dolonoid cavity. D. Internal view showing the internal openings of the tubules including the primary space within the dolonoid wall; this is the only specimen in which ordinary tubules communicate with the domicilial space. A–B × 40, C–D × 50.

phosis the dolonid pouch has developed further. This stage is represented by three different *Craspedobolbina* species in Figs. 26, 27, 30, 31, and 37.

The tubules in the dolonoid pouch cannot be traced externally. Seen in lateral view the swelling has reached the level of the velar edge and has begun to incorporate parts of the domicilial wall in the region of the anteroventral depression (which is not very pronounced in these species). The zygal arch is not yet affected, and there are no constrictions of the velar edge in front of or behind the pouch.

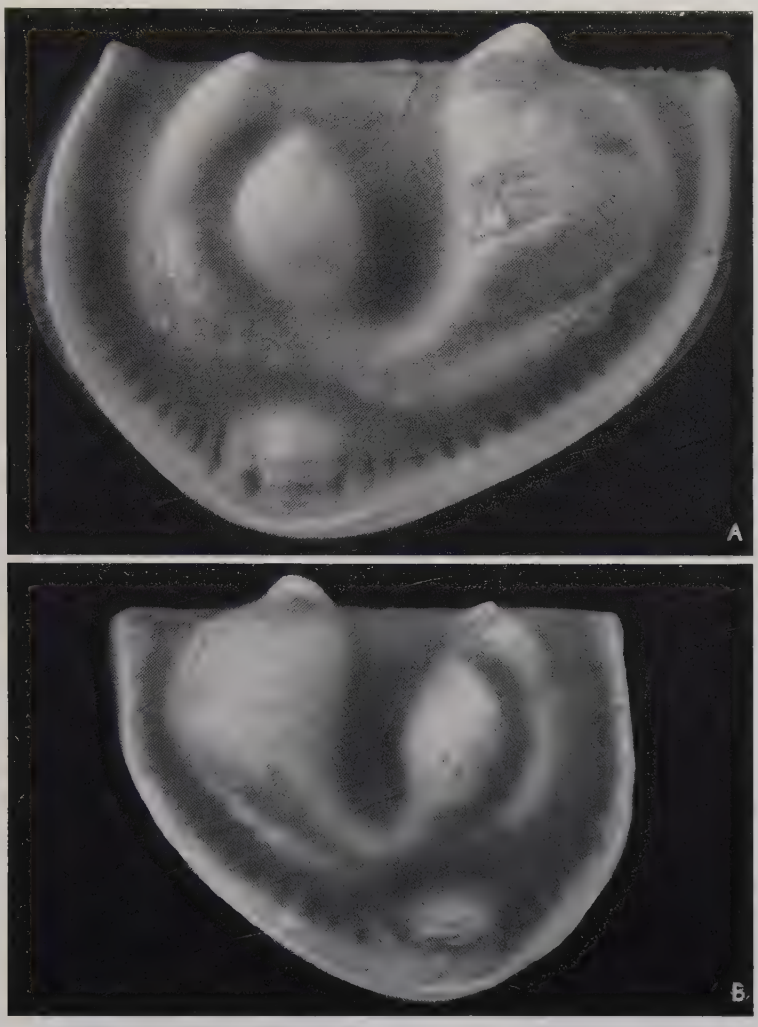
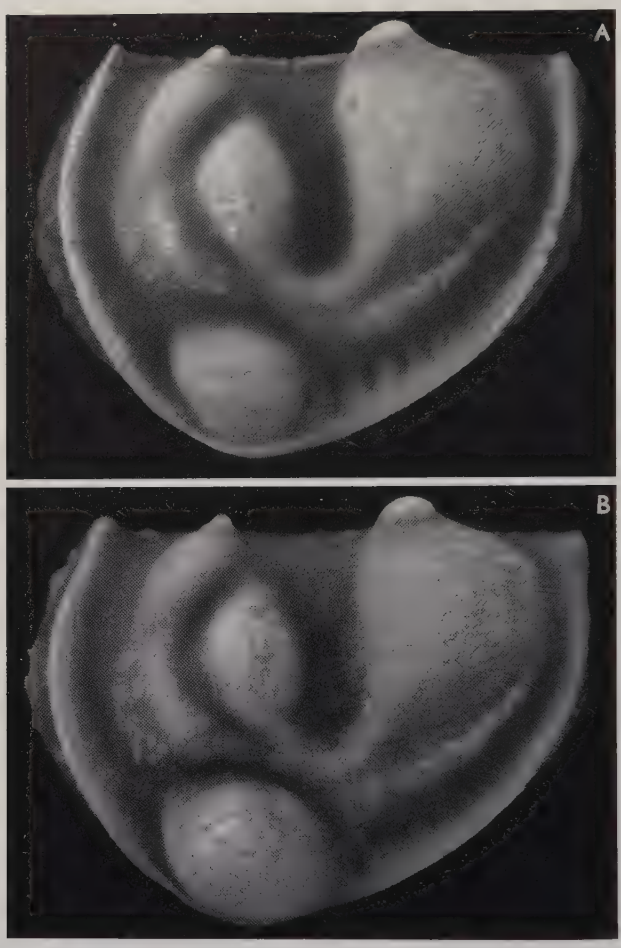


Fig. 29. Cruminal metamorphosis in *Craspedobolbina* (*Mitrobeyrichia*) *clavata* (KOLMODIN) interrupted at a very early stage. A. Specimen of adult size showing an enlargement of three anteroventral tubules, visible even in incident light. No. G 246. ×40. B. Specimen with dimensions of the penultimate moult stage. No. G 245. ×40. In both specimens the proximal ends of the tubules are closed.

The edge of the velum forms a broadly triangular flap which protrudes towards the vertical frill of the marginal structure which tends to disconnect itself from the covering frill by a narrow smooth area. At the base of the flap a ridge has been formed, merging with the velar edge towards its ends. This ridge persists even on the normal crumina of *Craspedobolbina* and *Hyrsinobolbina*. These conditions are best illustrated by Fig. 26: 2. The torus can still be seen on the inside of the velum along all the ventral part of the velar edge; it is however, more or less distorted by the extension of the flap (Fig. 31).



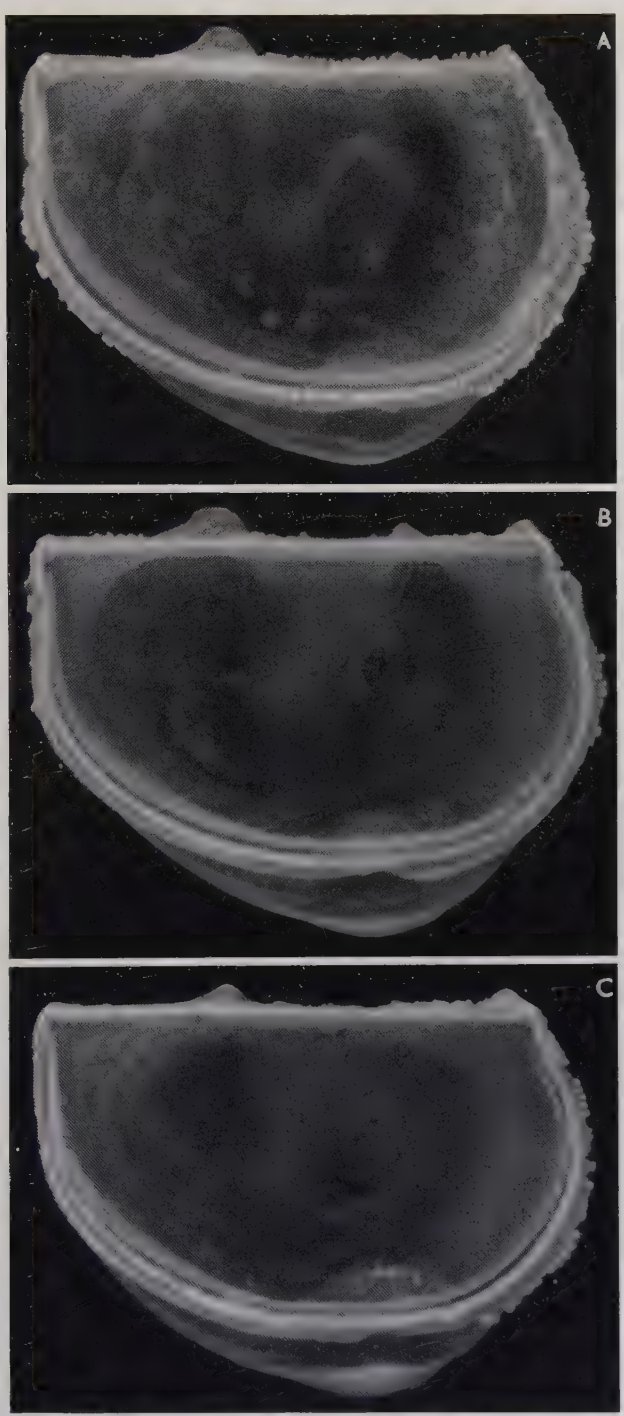
Craspedobolbina (*Mitrobeyrichia*) *clavata* (KOLMODIN), No. G 250. × 40.

Same species, No. G 252. × 40.

Fig. 30. Most cases of an incomplete cruminal metamorphosis have been interrupted at about this stage; as shown in the next figure it is in this stage that the flap is developed and begins to be bent inwards. The size often corresponds to the penultimate stage or is slightly larger; it is not known whether these specimens could moult once more in order to reach full size and obtain a compleletely developed crumina.

All normal tubules are closed towards the domicilium (Fig. 26: 3), but the three (it is uncertain whether this number is constant) tubules in the dolonoid part of the velum are marked as distinct depressions abmarginally; there is, however, no direct communication into the orimentary cruminal space which is now completely closed like the normal tubules.

At this stage the epithelial processes must have disappeared from the tubuli, and the innermost lining of the carapaces by calcium carbonate covers the former opening of the tubules evenly. Even the specialized tubules in the wall of the dolonoid pouch become more or less perfectly closed, probably not only by a simple formation of a new partitional wall but also by drawing up the



Same specimen as Fig. 30 A. Internal view. No. G 250. × 40.

Same specimen as Fig. 30 B. Internal view. No. G 252. × 40.

A third specimen the dolonoid flap of which is more strongly bent upwards and inwards. No. G 253. × 40.

Fig. 31. *Craspedobolbina* (*Mitrobeyrichia*) *clavata* (KOLMODIN). Development of the closing flap and former tubular openings in interrupted metamorphosis.

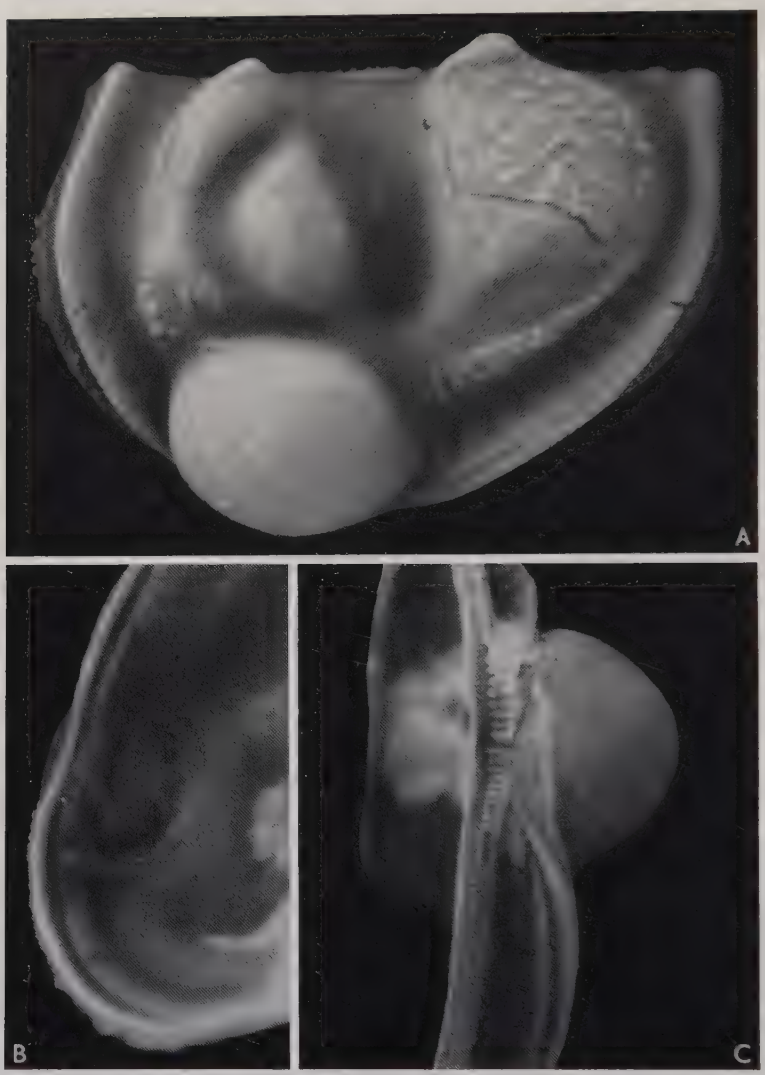


Fig. 32. Later interrupted cruminal metamorphosis in *Craspedobolbina* (*Mitrobeyrichia*) *clavata* (Kolmodin). Same specimen in all figures, No. G 254. × 40. A. Lateral view. The zygal arch has been reached by the inflation. B. Internal view (anterior end down), showing the thin area to be perforated after the closing of the dolonoid opening (i.e. which would not have been calcified if the metamorphosis had been complete). C. Oblique ventral view (anterior end up) showing that the flap has been bent up behind the vertical covering frill immediately before the insertion of the flap.

inner layer of the main velar fold towards the region of the abmarginal part of the circumference of the future cruminal opening (a stage slightly preceding that in Fig. 38 C).

A Late Dolonoid Stage.—A later stage is seen in Fig. 32. The dolonoid pouch is expanded so far that the zygal ridge has become obsolete.

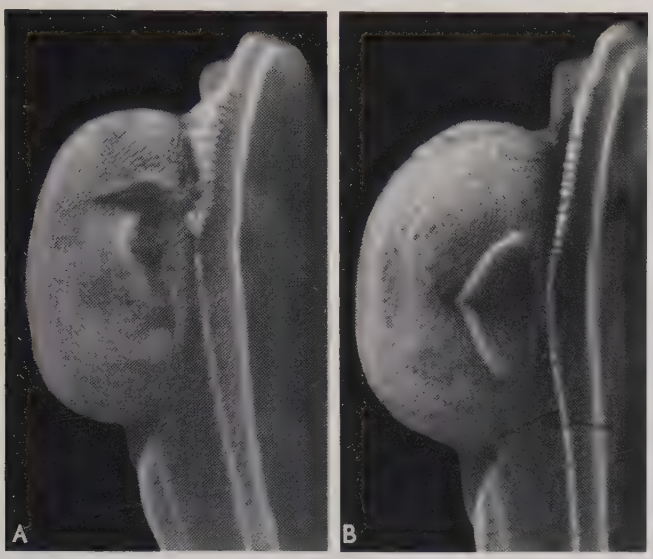


Fig. 33. The insertion of the closing flap has failed in these cruminae of *Craspedobolbina* (*Mitrobeyrichia*) *clavata* (KOLMODIN), probably owing to damage to the ventral side of the crumina. A. No. G 255. ×40. B. No. G 256. ×40.

The flap now is extended so far that it reaches below the edge of the vertical frill which is somewhat bent so that it lies in contact with the flap, covering its end. The dolonoid cavity is probably not considerably larger than in the preceding stages.

There is not yet an internal opening. The future communication between the crumina and the main part of the domicilium is, however, sharply set off by an ellipsoidal groove, and the partitional wall inside this groove is somewhat crumpled; probably it is very thin.

Intermediary cruminoid stages

There are a few specimens (cf. Fig. 33) in which the last stage in the cruminal metamorphosis, the insertion of the flap into the dolonoid cavity in contact with the admarginal part of its circumference, has failed. This is, however, due to the fact that the flap was subjected to some kind of exterior violence at the moment when the opening was closed.

There are, furthermore, a few cases where the closing of the crumina has been completed but the final expansion, more illustratively termed the *inflation*, of the crumina has failed.

More interesting for the illustration of the origin of the interior cruminal opening are, however, those few specimens where there are remains of a partitional wall in the opening. In these cases the wall has been perforated eccentrically so that a crescent-shaped, very thin part of it is left to cover the larger

part of the opening. This thin wall may be wrinkled (Fig. 36: 11). A normal specimen of *Craspedobolbina* has only small remains of the ends of the crescent left along that part of the circumference of the opening which is nearest to the margin of the valve (Fig. 36: 10). In *Apatobolbina*, however, the few specimens prepared in this way all have a well-developed wall between the main domicilial space and the crumina, broken through along the admarginal part of the circumference of the crumina (Fig. 35A).

Summary of the ontogenetic evidence of the cruminal metamorphosis

The stages described above represent in calcified carapaces a metamorphosis which normally involves only the softer parts of the animal, immediately after the last ecdysis. The stages are verified by specimens of adult size, but there are also specimens of the same size as moult stage 2. It is impossible at present to explain whether this depends on a general retardation of the growth of those specimens which could not complete the metamorphosis or whether the metamorphosis was prematurely initiated after the penultimate ecdysis and could not be completed.

In the *Craspedobolbininae* the metamorphosis involved (1) the formation of a dolonoid pouch in which, however, an intravelar space formed by one or a few of the open tubules in the velum is as important as the dolonoid cavity, (2) a closing of all tubules, even those forming the intravelar space, (3) a closing of the opening of the dolonoid cavity opening with a flap, (4) the inflation of the crumina, and (5) the secondary perforation of the partition formed between the crumina and the main space of the domicilium according to (2) and (4).

The metamorphosis implies two kinds of pouches and three kinds of pouch openings: (*a*) a cruminoid pouch in the velar fold, with a primary opening, (*b*) an atavistic dolonoid pouch, and (*c*) the cruminoid pouch with a secondary opening, formed by the secondary perforation of an atavistic roof over the tubule which is the unit in the velar fold forming the crumina.

The word atavism is used here in its classical sense; the completely functionless but very complicated closing of the dolon is verified by phylogenetical evidence. The phylogenetic and ontogenetic evidence above the level of the *Craspedobolbininae* shows that the closing procedure was abandoned in the amphitoxotidine branch of development and suggests that the closing of the velar fold or its tubules was also abandoned.

The dolon, then, forms an extravelar pouch, but the crumina is intravelar. Both are, however, closely related to each other, reflecting specializations in the reproductive organs localized to the anteroventral region in a primitive group of palaeocopes.

The metamorphic changes as reflected in calcified carapaces are summarized in Fig. 34. The three stages known from material of *Craspedobolbina variolata* are shown in Fig. 37. The development interpreted in semischematical cross

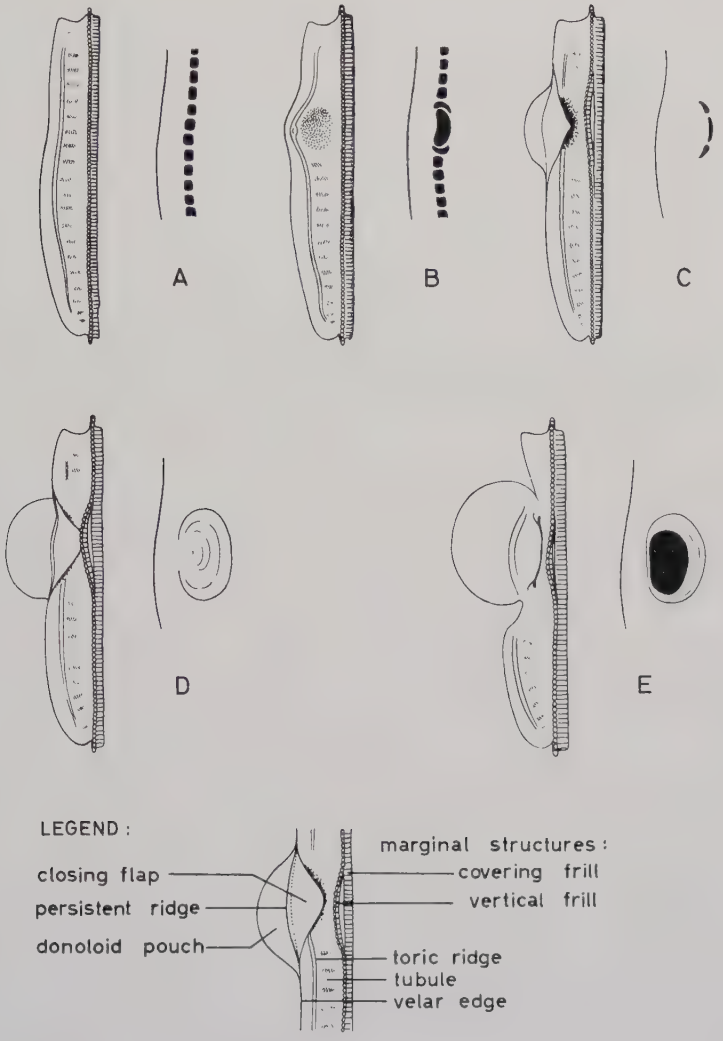


Fig. 34. Slightly schematic reconstruction of the cruminal metamorphosis in *Craspedobolbina*, expressed in terms of calcified carapaces. To the left of each valve seen in ventral view (protruding lobation omitted) the internal views of the same valves are shown. A. A valve in which the closing of the tubules has failed but no tubule is enlarged (incomplete tecnomorphic moulting, hypothetical). B. One of these tubules has become enlarged, filling the intravelar space of a dolonoid pouch with only a very shallow dolonoid space (cf. Fig. 28). C. The dolonoid flap has become enlarged and bends towards the dolonoid opening. Internally the tubules have been closed but small fissures remain in the tubules influenced by the dolonoid pouch (cf. Fig. 26:1–3, etc.) D. Insertion approaching completion; an oval area with a probably membraneous partition has been differentiated within the future margin of the cruminal opening (cf. Fig. 32). E. Cruminal metamorphosis completed exteriorly; in the cruminal opening there are wrinkled remains of the perforated membraneous partition (cf. Fig. 36:1, a normal cruminal opening is seen in Fig. 36:10).

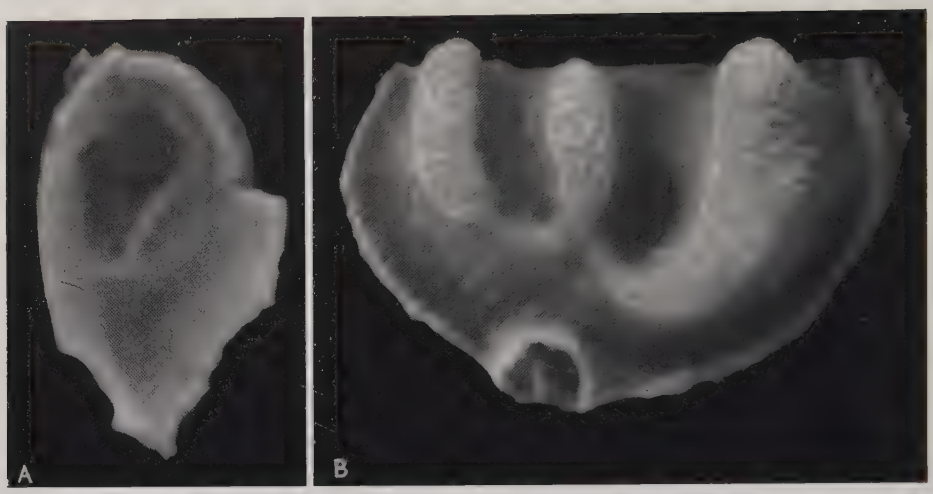


Fig. 35. A. *Apatobolbina gutnica* n.sp. Fragment of a right valve (anterior end up), showing the remaining partition between the crumina and the domicilium. No. G 291. × 50. B. *Juviella juvensis* n.sp. Some tubules have been inflated in the anteroventral region, but their proximal ends have been closed since the inflation of the crumina has failed at an early stage. Like the brittle distal parts of the normal tubules the distal part of the cruminoid swelling has been broken away. No. G 620. × 50.

sections is shown in Fig. 38. As no new cross-sections have been reproduced photographically in this paper, the reader is referred to the photograph published by Hessland 1949 (Pl. XIV, fig. 9) which shows an extraordinarily good preservation, without any considerable recrystallization of the adventral structures of a normal female specimen of *Craspedobolbina* cf. *clavata*, seen in front view.

The reader of a preliminary report on these questions (Martinsson 1960b) will find that a new stage in the beginning of the development has been introduced, showing that the cruminoid space was considerable all through the metamorphosis. This has resulted in a slight reinterpretation of the partition separating the crumina from the main domicilial space before the formation of the secondary opening (Martinsson, op. cit., Fig. 5B–C; Fig. 38B–C in this paper). The position of the inner layer of the dolonoid fold in the stage indicated by C in both figures quoted is in this case only of logical importance as it probably remained soft even if the metamorphosis was interrupted at this stage.

The new specimens have been obtained by selective extraction of some 400 kg of Mulde Marl. No additional calculation of the frequency of the intermediary stages has been made, but according to subjective observation their rareness in *Craspedobolbina clavata* was first slightly overestimated (cf. Martinsson 1960 b, p. 3).

Morphology of the primitive crumina

The primitive type of crumina is represented by the *Craspedobolbininae*. To summarize, this crumina is more or less globular, incorporating relatively little

of the carapace wall, causing constrictions of the adjoining parts of the velum (Figs. 25 and 37). There is a furrow, the dolonoid scar, left of the dolonoid opening, caused by the fact that a flap from the velar edge in this region was introduced and squeezed in it during the inflation of the crumina. The opening of the crumina was formed by a secondary perforation of a partitional wall, remains of which are sometimes found in the opening.

The carapace ornamentation does not extend onto the crumina. In some cases there is a fine striation of a part of the crumina which is formed by the outer layer of the dolonoid fold.

Branches of development

Starting from a crumina of the kind described above the beyrichiids treated in detail here can be divided into five different branches of development, each representing one subfamily. The *Kloedeniinae* (*Kloedeniidae*) are left out of consideration owing to lack of sufficiently detailed investigations showing their phylogenetic connections with the other branches (cf. p. 351 sqq.).

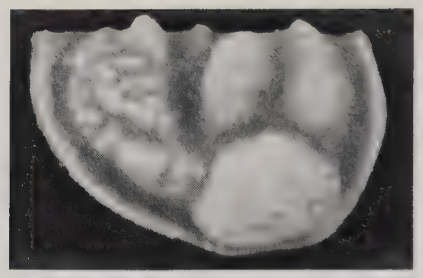
Already among the *Craspedobolbininae* there is a group of genera developing a very long sausage-shaped crumina along a considerable stretch of the ventral part of the velum; at the same time there is a reduction of the lobation. The crumina, however, does not incorporate much of the carapace wall. The typical fissure with the inserted flap is present in all these cases. A characteristic genus in this group is *Aitilia*. The opening of the crumina in this group has not been investigated.

The development of crumina in the family *Treposellinae* has also followed similar lines, but the velum does not take part in the metamorphosis to any considerable extent; it is not interrupted by the crumina which has incorporated large parts of especially the syllobial walls. The velum is mostly flange-like. In *Bolbiprimitia* and associated genera it is connected with the cruminal wall by two small bridges rather distant from each other, but the insertion of the flap has been abandoned. However, the step between the development in these genera and in the craspedobolbinine *Clintiella* is not very great.

In a Devonian group of treposelline genera, however, the site of the ontogenetic origin of the crumina is marked by a short furrow very near the edge of the velum. In the species most primitive in this respect, *Treposella lyoni*, it is even possible that the metamorphosis has passed a rudimentary dolonoid stage. In *Hibbardia* this short furrow has migrated towards the edge of the velum, and the velum forms two narrow bridges connected with the adjoining part of the crumina.

The genera in this subfamily form a morphological series with different degrees of lobal simplification and assimilation of the crumina with the lobes, from *Strepula* and *Treposella* to *Phlyctiscapha*.

The internal opening in one genus investigated, *Phlyctiscapha* (cf. KESLING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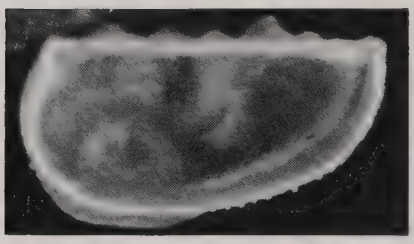
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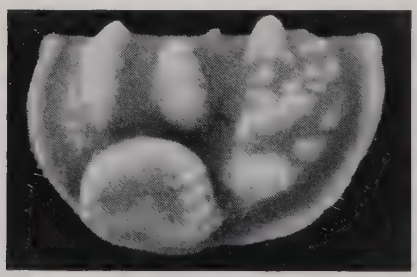
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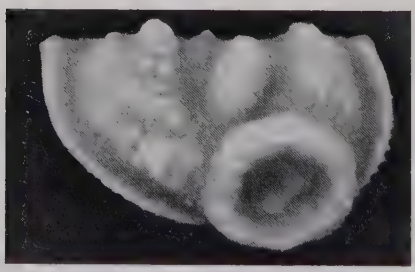
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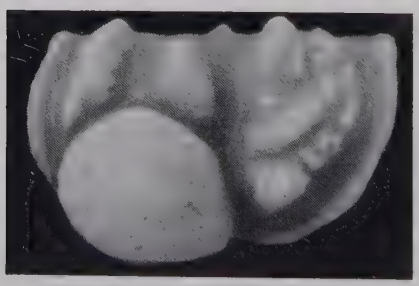
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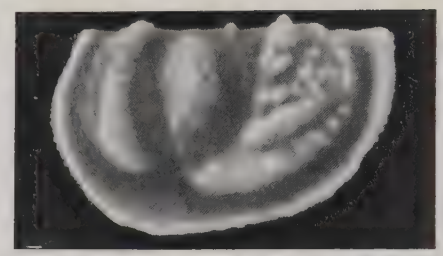
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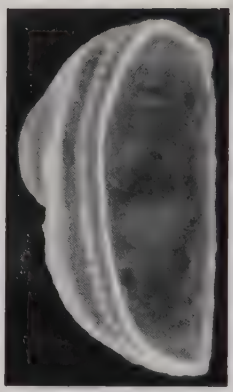
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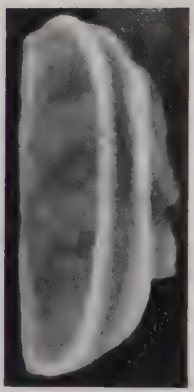
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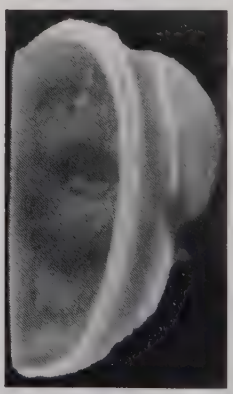
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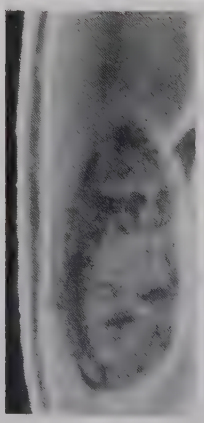
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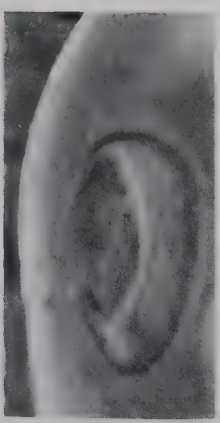
11

1953, Fig. 1), is restricted to the posterior part of the crumina; in *Bolbiprimitia* and *Hibbardia* there is a rod or strut across the anteroventral part of each valve, from the region of the end of the sulcus to a point just inside the edge of the valve (Fig. 96).

Turning back to the *Craspedobolbininae*, we find examples of a displacement of the rudimentary dolonoid pouch towards the distal part of the crumina, where it has shrunk to a minimum and the insertion of the flap may even be reduced to an impression of a very small part of the velar edge into the minimal dolonoid cavity, as in *Leptobolbina*.

The same development has gone much further along quite another line in the *Amphitoxotidinae*. In this subfamily the insertion of the flap has been entirely abandoned, but in more or less primitive forms the point of the velum situated on the most distal part of the crumina is more or less drawn up towards the ventral margin of the crumina.

In a primitive genus of this group, *Sleia*, which shows rather obvious relationships with the *Craspedobolbininae*, some intermediary stages in the cruminal metamorphosis are known (Fig. 36: 1–9). In this genus a velar flap is developed, but there is no dolonoid cavity, and the flap is not considerably bent down towards the valve margin (Fig. 36: 7–8). A specimen shows, however, that the internal opening is closed if the carapace becomes calcified before the inflation of the crumina (Fig. 36: 2). The inflation sometimes fails in this genus because the layers have difficulty in parting (Fig. 36: 3–4). The normal crumina has a ridge very like that in *Craspedobolbina* and *Hyrsinobolbina*, but in *Sleia* it is formed by the velar edge; the point of the former flap forms a small tubercle inside the ridge (Figs. 36: 9 and 42: 8). The amphitoxotidine crumina uses comparatively little of the carapace wall.

The ventral morphology of the crumina is much more varied than in the other subfamilies where it can provide constant characters for the entire subfamily or be common to two or more genera. In the *Amphitoxotidinae* trends illustrated by the following combinations can be found even within a single genus: (*a*) A narrow strip of the velum passes across the crumina but is distorted or pursed up into a small node at the side of the point of the velar flap, as in *Amphitoxotis* and *Hemsiella*. (*b*) The inflation has appropriated the anteroventral part of the velum so completely that there is nothing left of its edge or the torus

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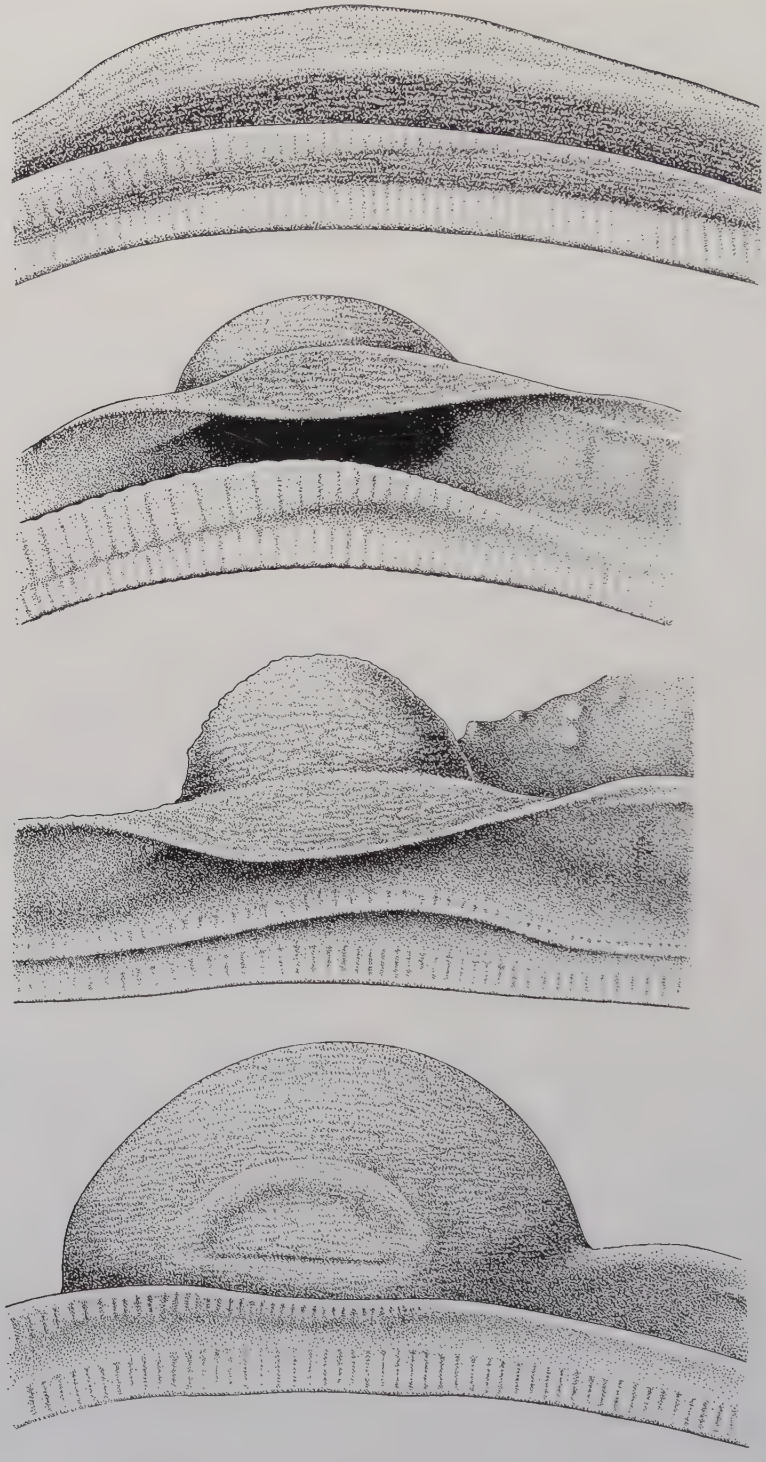
Fig. 36 (opposite page, reproduced from MARTINSSON 1960 b, Pl. V). 36:1–9. *Sleia equestris* n.sp. Dolonoid stage with considerably inflated but internally closed crumina (1–2, No. G 227). Dolonoid stages in which the inflation has failed, partly at least due to coherence of the layers of the velar fold (3, No. G 228, and 4, No. G 229). Completely developed female specimen (5, No. G 223) and normal tecnomorph (6, No. G 224). Velar edge of specimens with incompletely developed crumina (7, same as 1, and 8, same as 3; ventral view, anterior end up). Normal female left valve (9, ventral view, anterior end up). 36:10–11. *Craspedobolbina* (*Mitrobeyrichia*) *clavata* (KOLMODIN), internal views showing cruminal opening of normal specimen (10, left valve, anterior end down) and specimen with remains of a membraneous partition (11, right valve, anterior end up). 36:1–9 × 30, 36:10–11 × 45.



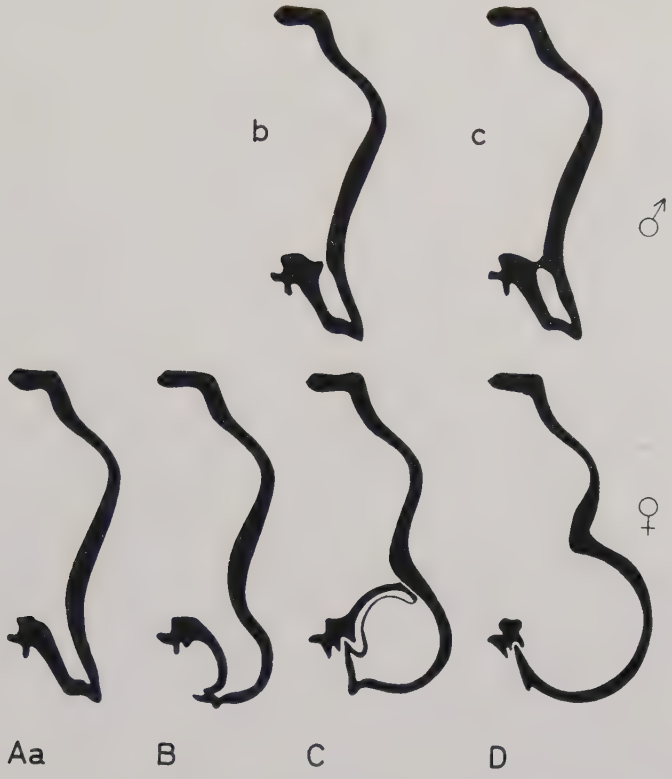


Fig. 38. Cruminal morphosis in *Craspedobolbina* expressed in terms of calcified carapaces and drawn without gradual increase in size. *Aa* is a tecnomorph calcified without the tubules being closed; *b* and *c* show the development of the normal tecnomorph. In *B* some anteroventral tubules have been enlarged, bending round the dolonoid space, and a closing flap has been developed. *C* shows the moment of closing, before the perforation of the cruminal opening. It is not known whether the inner layer of the velar fold remained in contact with the outer layer (cf. MARTINSSON 1960 b, Fig. 5 C) or was pressed apart from it during the inflation of the crumina, which is slightly more probable; it is very probable, however, that it did not become calcified. *D* shows the completed metamorphosis. A stage slightly later than *B* and stages corresponding to *c* and *D* have been verified by thin sections.

on the relatively considerable crumina, as in *Atterdagia* and *Hammariella pulchrivelata*. (*c*) The relatively small crumina in some advanced forms occupies only the proximal anteroventral part of the velum which passes undisturbed across it; the same may also be the case with the torus, as in *Berolinella steusloffi*.

The degree of inflation of the velum into a crumina is, then, the factor determining whether the velum is to reach onto or across the crumina; a

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Fig. 37 (opposite page, Fig. 2 in the preliminary report, MARTINSSON 1960 b). *Craspedobolbina* (*Mitrobeyrichia*) *variolata* n.sp. Tecnomorphic valve (No. G 207), reconstruction of dolonoid stage seen in two different inclinations (No. G 205), and a normal crumina (No. G 208). Left valves, anterior end to the left. × 80.

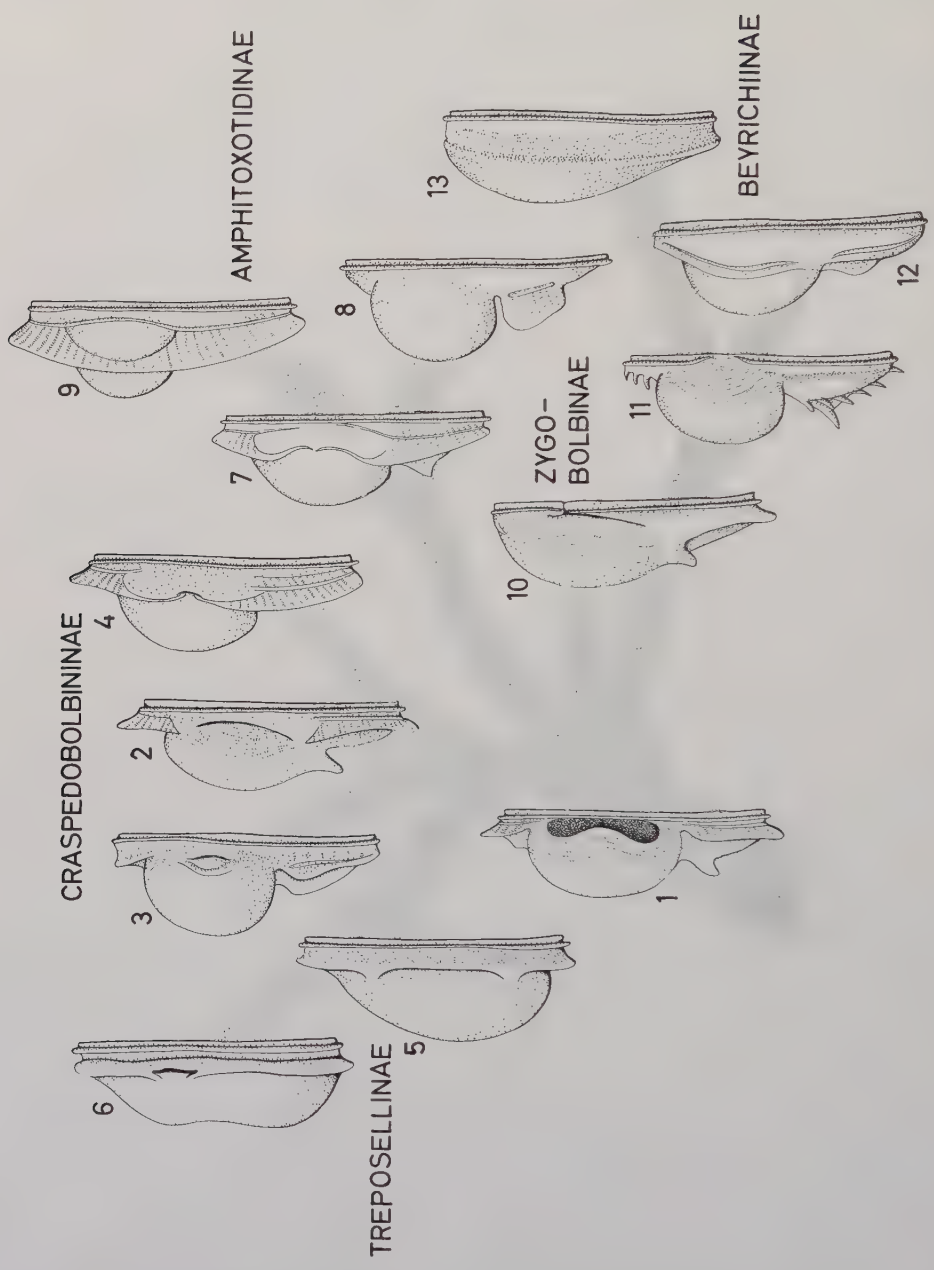

Fig. 39. Generalized diagram showing the lines of cruminal development illustrated by the beyrichiid subfamilies represented on Gotland. 1. A hypothetical representative of the dolonate ancestors, "beginning" to close the dolonal pouch with a flap; the edges of the vela were probably not in contact with each other. 2. A primitive craspedobolbinine in the *Aitilia–Hamulinavis-Clintiella* group of genera. 3. *Craspedobolbina* and *Hyrsinobolbina*. 4. An advanced representative of the *Apatobolbina–Leptobolbina* group in which the dolonoid remains have migrated to a more distal point of the crumina and approach obsoletion. 5. Silurian *Treposellinae* of Europe with widely separated treposelline bridges. 6. Devonian *Treposellinae* of America

secondary growth of a velum across the brood pouch (KESLING 1957b, p. 64) does not take place.

The *Zygobolbinae* follow another line of development from forms with a primitive dolonoid flap. The distal part of the edge of a reduced dolonoid flap was probably folded over and through the valve margin during the metamorphosis of the soft parts. In the calcified valve the fold or fissure marking the closing of the crumina breaks through both the extramarginal shelf and the marginal structure. The details of this procedure are unknown.

In the *Beyrichiinae* the margin of the valve inside the crumina was also affected in primitive forms, but there is never a fissure or fold near it; however, the marginal structure very often becomes obsolete in the cruminal region. Like the *Zygobolbinae* representatives of this family have a finger-print striation on the ventral part of the crumina, which is mostly more or less globular and incorporates elements of the carapace wall and retains elements of the carapace ornamentation. In some advanced *Beyrichiinae*, however, the crumina is so assimilated with the lobation that it is seen only as a fairly gradual swelling towards the anteroventral part of the carapace. In another advanced but more distinctly lobate genus, *Navibeyrichia*, both a velar ridge and a torus pass the crumina without interruption.

The ventral morphology of the crumina also exhibits a covariation with other lobal and ornamental characters than those included above. They are found in the descriptions of the different subfamilies and genera.

Individual descriptions of intermediary stages in the cruminal metamorphosis

The present conception of the cruminal metamorphosis is founded on the material briefly described below. Only a few specimens have interrupted the metamorphosis at very similar stages; the others form a very continuous series of stages all through the procedure. However, it would be desirable to document the very early and very late dolonoid stages better even in *Craspedobolbina* and to bring the ontogenetic knowledge on the other subfamilies to the same level as in the *Craspedobolbininae*. The investigation of material prepared in three dimensions like the present leaves little to be desired, but undoubtedly it would be desirable to make thin sections through a dolonoid pouch in the

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with an anteroventral scar in the thick velar ridge. 7–9. Different phylogenetic stages in the occupation of the velar fold by the cruminal space, more or less homoeomorphically appearing in different branches of the subfamily, having a deflected velum with or without a distal constriction on the crumina, as in *Amphitoxotis* and the English Wenlockian *Amphitoxotidinae* (7, also features from *Sleia*-like ostracodes, such as the spur), filling out the velum completely, as in *Atterdagia* and *Hammariella* (8), or only partly, as in *Berolinella steusloffi* (9). 10. Primitive zygobolbine, synthesized from *Slependia*, *Noviportia*, and *Zygobolba*. 11. *Beyrichia–Neobeyrichia* stage. 12. *Gannibeyrichia* stage. 13. *Navibeyrichia* stage. The correlation of lobal and cruminal features has aided the determination of the branching points; the length of the branches is, naturally, highly subjective.

stage where the enlarged tubule inside the wall of the dolonoid pouch is being partitioned off from the domicilium.

The individuals below have been arranged in approximately the order indicated by the stage in which the metamorphosis has been interrupted; this is not always completely congruous with the increase in size of the dolonoid pouch. The dimensions given are the length of the hingeline (HL) and the height over the adductorial sulcus from the level of the velar edge immediately behind the dolonoid pouch or crumina (SH). "Subadult" indicates that the specimen has the size of the moult stage preceding the adult.

Craspedobolbininae.—(1) *Craspedobolbina clavata*, fragment of a right valve, subadult, No. G 243, Mulde. External bulge of the dolonoid pouch very small; edge of the orimentary flap not yet bent in medioventral direction; torus flattened nearest to the cavity, with a shallow pit; cavity very shallow. Tubules open at proximal end; the central tubule in the dolonoid wall much enlarged, with a reniform opening, compressing the lumen of adjoining tubules.

Matrix removed from all sides; even tubules freed from marl by needle preparation. Marl particles somewhat dispersed in a granulous mass of recrystallized calcite in the critical region of the openings of the tubules, when the first openings had been exposed utmost care was used in order not to damage a possible cover of the others. Fig. 28, cf. p. 92.

(2) *C. clavata*, right valve, HL 1715 μ, SH 1295 μ (large subadult or small adult), No. G 244, Mulde. External dolonoid bulge considerably larger than in preceding stage; flap more strongly pointed but not bent; torus extends into the distal part of the dolonoid cavity. All normal tubules of the velum closed; the central tubule in the dolonoid wall just being closed; a semicircular furrow pierces deeply into it.

Matrix removed from interior and subvelar field.

(3) *C. clavata*, right valve, HL 1695 μ, SH 1230 μ (large subadult), No. G 245, Mulde. External dolonoid bulge smallest observed; tubules to be seen in it in transmitted but not in incident light; flap not bent; torus passes indistinctly the distal part of the cavity; cavity very shallow. All tubules closed; tubules of the dolonoid wall almost without traces in the interior of the valve (certainly due to the small size of the tubules).

Matrix removed from lateral and subvelar fields, and the ventral part of the interior. Fig. 29 B.

(4) *C. clavata*, left valve, HL 2075 μ, SH 1565 μ (large adult), No. G. 246, Mulde. External bulge very small; three tubules distinctly marked on it, seen even in incident light; flap inconsiderable, not bent; dolonoid cavity shallow. All tubules closed as in the preceding specimen.

Matrix removed except in preadductorial node and lobal cusps. Fig. 29 A.

(5) *C. clavata*, left valve (posterior cardinal corner broken off), HL 1695 μ, SH 1270 μ (subadult), No. G 251, Mulde. Dolonoid bulge reaching just below the zygal ridge but distinctly separated from it; flap very little pronounced, but the adjoining parts of the velar edge form a bow in marginal direction; torus uninterrupted; cavity quite deep. A semicircular groove marks the site of former tubules in dolonoid wall.

Matrix removed except in lobes and in the innermost part of the dolonoid cavity.

(6) *C. clavata*, right valve, HL 1710 μ, SH 1265 μ (large subadult), No. G 247, Mulde. External bulge reaching just below the zygal ridge but distinctly separated from it, without traces of tubules; flap still seen in lateral view, very slightly bent, ornamental crest below the bulge still distinct; depth of cavity and morphology of torus not observed. Slight furrow inside the contact of the dolonoid wall.

Matrix removed from exterior and interior; left between the dolonoid cavity and the marginal structure.

(7) *C. clavata*, right valve, HL 1695 μ, SH 1365 μ (large subadult), No. G 248, Mulde. External bulge and flap almost as in the preceding specimen, distance between zygal ridge and bulge slightly larger; cavity quite deep; details of torus not observed.

Matrix removed from lateral and subvelar fields except dolonoid cavity; interior not prepared owing to difficulties caused by recrystallization.

(8) *C. clavata*, right valve, HL 1945 μ, SH 1595 μ (adult), No. G 249, Mulde. External bulge, flap, and ornamental ridge similar to preceding specimen; flap somewhat smaller and inconsiderably bent; the adjoining parts of the velar edge, however, form a more distinct curve towards the velar margin; concavity rather shallow; torus passing it without interruption.

Matrix removed from lateral and subvelar fields except from the deepest part of the dolonoid cavity; interior not prepared owing to difficulties caused by calcite crystallization.

(9) *C. clavata*, left valve, HL 1665 μ, SH 1430 μ (subadult), No. G 250, Mulde. External bulge, flap, etc. similar to preceding specimen; torus still passes between the cavity and the velar edge without interruption; cavity rather shallow. Intravelar space formed by tubules in the dolonoid wall large, former openings of tubules marked by a distinct semicircular furrow.

Matrix entirely removed. Major cracks across the valve. Figs. 30A and 31A.

(10) *C. clavata*, left valve HL 1930 μ, SH 1365 μ (adult), No. G 252, Mulde. Morphology of the crumina slightly more advanced than in the preceding stage; the bulge almost in contact with the zygal ridge; flap not seen in lateral view, almost ridgelike but projecting inwards; cavity deep but flattened; torus still seen inside the flap. Tubules in the dolonoid walls marked as a crescent-shaped furrow.

Matrix almost completely removed, even in the dolonoid cavity. Figs. 30B and 31B.

(11) *C. clavata*, left valve, HL 1610 μ, SH 1310 (subadult), No. G 253, Mulde. Main features identical with those in the preceding specimen, but the flap now projects definitely in the direction of the margin; the flap forms a very obtuse triangle with its base along the ornamental ridge; cavity as in the preceding stage. The internal furrow is deep and crescent-shaped.

Matrix removed from all parts. Fig. 31C.

(12) *C. clavata*, fragmentary left valve, large subadult size, No. G 216, Mulde. External features almost exactly like the preceding stage; the inflation has reached almost equally far in all specimens (4)–(12); torus interrupted in the dolonoid cavity; exterior ornamental ridge very pronounced along the base of the flap. Deep internal crescent-shaped furrow with two constrictions between three deeper sections.

Matrix removed from all parts. Figs. 26: 1–3.

(13) *C. clavata*, left valve, divided into two parts originally kept together by the matrix, HL 2065 μ, SH 1500 μ (adult), No. G 254, Mulde. Dolonoid pouch inflated so that the zygal ridge has been incorporated; flap strongly extended and inserted behind the vertical frill of the marginal structure. Future cruminal opening distinctly marked; partition forming a very irregular surface within the area of the future opening.

Matrix removed from all parts except lobes and the inaccessible dolonoid cavity. Fig. 32, cf. p. 98.

(14) *C. clavata*, right valve, HL 1965 μ, SH 1265 μ (adult), No. G 255, Mulde. The specimen is normally developed except that the insertion of the flap has failed, probably owing to some kind of injury causing an extra transversal fold from the anterior part of the flap; the flap is folded into the crumina along the ornamental ridge. Remains of the partition fringe the entire circumference of the cruminal opening. Fig. 33A.

(15) *C. clavata*, fragmentary left valve, adult, No. G 256, Mulde. Normally developed, except that the flap has failed in closing the dolonoid owing to a transversal fold, probably caused by injury; the fold also breaks the ornamental ridge. Interior not prepared and investigated as the two main parts of the broken valve are kept together by the matrix. Fig. 33 B.

(16) *C. clavata*, entire carapace, HL 1815 μ, SH 1430 μ (small adult), No. G 256, Mulde. The only complete carapace known showing intermediary stages of the cruminal metamorphosis; at the same time the only specimen known showing asymmetry in the development of the cruminae. Development of left crumina interrupted at a very early dolonoid stage, right crumina has reached the stage of the insertion of the flap. Both dolonoid pouches, as well as other parts of the vela, with furrows and distortions of pathological or teratological origin.

(17) *C. variolata*, fragmentary left valve, adult, No. G 205, Svarvare. Early dolonoid stage, incorporating very little of the carapace wall. The flap has in this species a very broad base; in the present specimen it is already bent down towards the vertical frill of the marginal structure which makes a distinct bend towards the dolonoid opening. Ornamental ridge distinct; the pattern of subconcentric striae present in dolonoid pouches in *Craspedobolbina* is extraordinarily distinct. Dolonoid cavity relatively large. A crescent-shaped furrow marks the obsolete tubular openings.

Matrix removed from all sides of the dimorphic region; preparation very complicated owing to the fact that calcareous matrix fragments were firmly attached to the valve by recrystallization. This was the first intermediary stage found (Martinsson 1960b). Figs. 26: 5, 27: 1–3, 37, and 53.

(18) *C. variolata*, left valve, HL 1830 μ, SH 13330 μ (adult), No. G 257, Svarvare. Insertion of the flap completed, but inflation has failed. Zygal ridge not reached by the incorporation of the carapace wall with the crumina. Fig. 61 b.

(19) *C. variolata*, fragmentary right valve, adult, No. G 258, Svarvare. Normal exterior. The cruminal opening partly covered by a crescent-shaped membrane, slightly narrower than that shown in Fig. 36: 11.

(20) *C. acuminulata*, left valve, HL 1230 μ, SH 1030 μ (adult), No. G 217, Follingbo I. Dolonoid pouch in early stage, not affecting the zygal arch; flap constituted by a fairly narrow extension of the anteroventral part of the velar edge, slightly bent. Crescent-shaped furrow interiorly, inside the base of the dolonoid pouch.

Matrix removed except in dolonoid cavity, Valve glued together from two fragments. Fig. 27: 4–5.

(21) *C. acuminulata*, left valve, HL 1415 μ, SH 970 μ (adult), No. G 218, Follingbo I. Dolonoid pouch almost reaching the junction of the zygal ridge with the preadductorial node; flap not very distinct; the velar margin, however, is slightly curved inwards in the anteroventral region. Interior crescent-shaped groove present.

Interruption of metamorphosis probably caused by injury to the pouch near the zygal arch.

Matrix removed from all parts except dolonoid cavity. Fig 27:6–7.

(22) *C. acuminulata*, right valve, HL 1400 μ, SH 885 μ (adult), No. G 259, Follingbo I. Normal, except that the metamorphosis has been interrupted at the moment of the insertion of the flap; the inflation has failed. The crumina is almost fused with the zygal arch.

(23) *C. unculifera*, fragmentary right valve, adult (?), No, G 260, Bingers. Very small dolonoid pouch, not affecting the zygal arch. The flap, however, is strongly bent down towards the dolonoid cavity.

The state of preservation, in a strongly cemented "sedimentary microbreccia" of calcareous fragments, does not allow further observation.

Amphitoxotidinae.—(24) *Sleia equestris*, right valve, HL 1575 μ, SH 965 μ, No. G 227, Sles. Dolonoid pouch very large, reaching the preadductorial node. A flap has been formed and is slightly bent inwards; the torus continues onto its inner side. There is no dolonoid cavity. The cruminal space is very large; the partition between the crumina is marked by an almost ellipsoidal groove.

Matrix entirely removed. Figs. 36: 1–2 and 36: 7.

(25) *S. equestris*, left valve, HL 1530 μ, SH 1005 μ (adult), No. G 228, Sles. Slightly more advanced stage than the preceding, but the inflation of the crumina has failed as the two layers of the velar fold have not parted. Exteriorly, this results in a curved sausage-shaped inflation of that part of the crumina which is formed by the distal parts of the dolonoid extension of the velum. The opening of the crumina has been developed.

Matrix completely removed. Figs. 36: 3 and 36: 8.

(26) *S. equestris*, right valve, HL 1595 μ, SH 965 μ (adult), No. G 229, Sles. The incorporation of elements in the carapace wall is maximal, and the velar elements are engaged to such a degree that the velum is somewhat constricted in front of and behind the crumina. The inflation, however, has failed, owing to the coherence of the distal and central parts of the outer layer of the dolonoid part of the velum with the inner layer. The resulting crumina is almost completely ring-shaped.

Matrix completely removed. Fig. 36: 4.

(27) *Juviella juvensis*, left valve, HL 1280 μ–SH 870 μ (subadult), No. G 620, Hoburgen Ia. A few tubules have been inflated, but the inflation has been interrupted at an early stage, and the tubules have been closed proximally as the normal tubules; there is a somewhat curved furrow marking the closed openings. The incorporation of wall elements in the anteroventral depression is inconsiderable.

Matrix removed laterally and from other parts of the cruminal region. Fig. 35 B.

Beyrichiinae.—(28) *Beyrichia* (*Beyrichia*) *bicuspis*, left valve, HL 1510 μ. SH 1085 μ (small adult??—subadult), No. G 261, Follingbo I. Anteroventral part of the velar bend much thickened; the thickening covers the extramarginal shelf and is distinctly set off from the lateral side of the wall. There is only a very shallow furrow in the interior of the dolonoid part of the velar ridge, and the swelling is, therefore, probably solid.

There is no objective confirmation that this swelling is an early stage in the development of the beyrichiine crumina. It is extremely improbable, however, that the specimen is pathological. It is in an excellent stage of preservation.

Matrix completely removed from the interior as well as from the exterior. Fig. 147 F.

Origin of beyrichiid ostracodes

Theories on the origin of the *Beyrichiidae* could not be formed until the systematic consequences of the difference between the beyrichiacean crumina and the dolonal pouch in other palaeocopes were realized. Though the main features in the morphology of the two kinds of pouches had been known to earlier writers (cf., e.g., Ulrich & Bassler 1923, p. 278), a reconsideration of the brood pouch problem by Hessland (1949, pp. 123–128) provided the decisive impetus towards a restricted family *Beyrichiidae*, characterized by the cruminal dimorphism (Henningsmoen 1953, pp. 196 and 235–238). The systematic importance of the dimorphic characters was still more stressed after an analysis of palaeocope dimorphism by Jaanusson (1957), who excluded all non-cruminate taxia from the superfamily *Beyrichiacea*.

The distinction between the two kinds of pouches is, however, not too successfully made even in recent papers. The crumina certainly incorporates considerable parts of the carapace wall, but it is not logical to distinguish between "velar pouches" and "pouches formed by the carapace wall". Nor are the ethical and functional aspects expressed as "false pouch" *versus* "brood pouch" recommendable, especially as it may now be urged that the false pouch is the true one.

Especially for a phylogenetic discussion it is important that the terms used do not conceal the existing homologies. Below, as well as in the preceding discussion, the term *dolonal pouch* is used for the special case in which the dolon of a normally developed female forms a pouch; a *dolonoid pouch* is the corresponding atavistic structure in incompletely developed beyrichiid females; the domicilial, basically intravelar pouch derived from it is called the *crumina*.

(For practical reasons it should be pointed out that the quantity of the *i* in *crumīna* (Lat. purse) is long and that the word consequently should be stressed on the penultimate syllable. The rare—and purer—writing *crumina* has been preferred to the more common *crumena* as it forms a more attractive stem for the adjective *cruminal*.)

Theories based on phylogenetic evidence

The similarity of the *Beyrichiidae* to some eurychilinacean ostracodes, especially the eurychilinid genus *Chilobolbina*, is very striking. This similarity is stressed also by some of the new genera published here. The tecnomorphs of *Clintiella* would hardly have been recognized as beyrichiids if the females had not been present, and the dimorphic pouch in *Clintiella* and *Barymetopon* would not immediately have been recognized as a crumina if its ventral side had not been accessible. *Apatobolbina* was long a genus in which the nature of the pouch opening was not known.

Since the systematic importance of these problems was realized, several writers have summarized their opinions derived from the evidence provided by different palaeocope forms found through the Ordovician and Silurian. They are the following (in order to avoid confusion page references have been omitted within the quotations):

Hessland 1949 (p. 127): "The egg-shaped pouch of *Chilobolbina* may not have been very suited to prevent deep sinking in the mud. It is also unfit as a brood space though not so impossible as the *Eurychilina* type. With respect to typology, it is intermediate between that of the *Eurychilina* type and that of *Beyrichia kloedeni*. It may be questioned whether it really, but exceptionally, could be utilized as a breeding pouch. It may be of interest that the type of pouch which was practically impossible as a brood pouch (the *Eurychilina* type) is that which first appears geologically (Lower Ordovician). The one which most certainly served as a breeding space (*Beyrichia kloedeni*) is the youngest one (Gotlandian). The intermediate type (*Chilobolbina*) is of intermediate age (Middle Ordovician)."

Henningsmoen 1953 (pp. 200–201): "It still seems uncertain whether the Beyrichiidae

developed from the Eurychilinidae (as is often suggested) or some other Ordovician family ... The Silurian beyrichiid faunas are especially characterized by the dimorphic swellings of the Beyrichiidae and Kloedenellidae."

HENNINGSMOEN 1954 (p. 34): "It is generally assumed that the beyrichiids developed from the eurychilinids. This appears to be rather probable, as early beyrichiids have much in common with species of *Platybolbina*."

HENNINGSMOEN 1955 (p. 241): "*Craspedobolbina dietrichi* Kummerow, 1924 from a glacial drift boulder of probably late Ordovician limestone in northern Germany, is possibly the earliest known beyrichiid. It reminds one of primitiids and eurychilinids, from which the Beyrichiidae may have developed, but it also reminds one of *Beyrichia* (*Eobeyrichia*) and the *Zygolbolbinae*, with which it shares a zygal ridge."

JAANUSSON 1957 (p. 223): "According to HENNINGSMOEN the beyrichiids probably developed from the eurychilinids. As the construction of their velar structure seems to be almost identical this assumption appears to be very likely. The velar frill of both eurychilinids and certain beyrichiids is partitioned radially into a number of internal, hollow, tube-like chambers, and this construction of the frill is unknown in other palaeocopes except for *Oepikium* and the puzzling recent family *Punciidae*. The general appearance of the tecnomorphs of certain non-or unisulcate genera of *Eurychilinidae* and *Beyrichiidae* is remarkably similar. The development of the beyrichiids from the eurychilinids involved, however, loss of the external, velar dimorphism and formation of an internal, cruminal dimorphism. Until the course of these important changes is properly understood the exact degree of relationship between these families cannot be said to be known."

KESLING 1957 b (p. 71): "1. During Lower Ordovician time certain eurychilinid ostracods developed strongly convex frills.

2. During Middle Ordovician time dimorphism in the form of the frill appeared in the descendants of the eurychilinids, the piretellids. This dimorphism, as Hessland suggested, may have evolved as a necessary adaption in the female for copulation with the wide-frilled male. The frills of female piretellids became so strongly convex that their edges met to form false pouches.

3. One genus of piretellids, *Chilobolbina*, developed a bulbous false pouch that was curved inwards at its distal margin.

4. During very late Ordovician or early Silurian time the beyrichiids developed from the piretellids when the distal edge of the false pouch fused with the contact margin to form a brood pouch. Probably at the same time, a part of the valve wall enclosed by the brood pouch receded from the contact margin to produce an opening from the interior of the valve to the brood pouch. The remaining part of the valve wall served as a partition between the pouch and the rest of the valve. The internal structures described in beyrichiid females are relics of the ancestral valve wall.

5. The use of the beyrichiid pouch for brood care may have started quite fortuitously when the young instars took advantage of the protection it afforded. Beyrichiids show no progressive enlargement of the brood pouch, such as one might expect if these structures were developed for the purpose of accommodating the immature offspring."

There is universal agreement among writers that the phylogeny of the beyrichiids proceeded *via* forms with an anteroventral, incurved dolon and forms with a closed anteroventral dolonal pouch. HENNINGSMOEN's and KESLING's discussion is largely characterized by the premises that the development has proceeded *via* known and named taxia found as fossils in the stratigraphical sequence according to the chronology of development.

If the phylogenetic evidence is supplemented with ontogenetic evidence, the large trends outlined are strongly confirmed, but the detailed view of the development is altered in many points, in many cases radically.

Ontogenetic evidence

The cruminal metamorphosis which is the last phase in the ontogeny of the *Beyrichiidae* recapitulates essential features in the phylogeny of the palaeocope branch which comprises, at least, the *Eurychilinacea* and the *Beyrichiacea*. Primitive *Beyrichiidae*, as the *Craspedobolbininae*, do this more completely than advanced forms. In other words *the cruminal metamorphosis displays a palingenetic development which is most complete in the genus* Craspedobolbina; *hence this genus includes the most primitive beyrichiids known.*

The ontogenetic documentation is already presented in detail above. It leads to the following interpretation.

The *Beyrichiacea* originated from forms developing an anteroventral dolonal pouch like that of known *Eurychilinacea*. It is not necessary to presume that the margins of these dolonal pouches were in contact with each other as in *Chilobolbina*; it is more probable that *Chilobolbina* represents its own branch of development towards a pouch which could be completely closed when the valves were closed. In the beyrichiacean branch the crumina was closed in later forms by a flap of the velar edge, inserted into the opening of the former dolonal pouch. In the primitive beyrichiacean the cruminal space came into communication with the domicilial space by a secondary perforation of the roof of the crumina.

The most primitive beyrichiids display these conditions. But within the *Beyrichiidae*, as already described in the ontogenetic sections above, there are several trends, some of them essentially similar in different developmental branches, towards a simplification in the metamorphosis and morphology of the crumina. They lead (a) to the abandonment of the dolonoid cavity and of the insertion of the flap, (b) to a direct inflation of the dolonoid part of the velum into a crumina, and (c) to the enlargement of the crumina by filling out larger parts of the velum or (d) incorporating large parts of the carapace wall, locally in the anterior part of the valve or even influencing the greater part of the ventral part of the valve, including the syllobium.

The present interpretation differs from earlier ones in several respects. They are shortly reviewed here:

(1) There is no obvious trend in the size within the *Beyrichiidae* indicating the size of the ancestors. Within the family, though, there is a trend to simplification of the lobation by fusion of the primitive preadductorial knob with a primitive anterior lobe, resulting in forms with an anterior lobal complex and a syllobium divided by one sulcus; finally even the sulcus may become obsolete (*Craspedobolbininae – Treposellinae*; similar trends are found in the *Beyrichiinae*).

There is also a trend to reduction of a broad tubulous velum into a velar ridge without tubules and to incorporation of carapace parts, starting from the anteroventral part of the valves (cf. KESLING 1957b, pp. 62–63).

(2) *Craspedobolbina* is regarded as a primitive beyrichiid but with quite a different definition of the genus and other views on the age of *C. dietrichi* than in earlier papers (KUMMEROW 1924, p. 427; Pl. 20, figs. 27–28; SCHMIDT 1941, p. 27, foot-note 1; HENNINGSMOEN 1954, pp. 35 and 48; HENNINGSMOEN 1955, pp. 241–243, KESLING 1957b, p. 63). KUMMEROW's extant material and the tecnomorph figured by KUMMEROW (l.c.) show that *Craspedobolbina* and *Beyrichia* (*Mitrobeyrichia*) HENNINGSMOEN are synonyms (cf. pp. 34 and 146); there is no reason to believe that the species is Upper Ordovician, as very closely related forms are all Silurian. Even if KUMMEROW's drawing (l.c.) of the female is correct, with a sulcus behind mid-length and a zygal arch not influenced by the crumina—which is very improbable—the craspedobolbinines are not closely related to the group represented by *C. armata* HENNINGSMOEN which is here referred to the *Zygobolbinae*.

(3) There are internal structures in connection with the cruminae in some *Treposellinae*. In *Phlyctiscapha* there is a partition screening off the anterior part of the crumina from the domicilium (KESLING 1953). In *Hibbardia* there is a rod-like structure placed as a strut across the crumina in the adductorial region (KESLING 1957a). There is a similar structure in *Bolbiprimitia* (p. 210). The partition demonstrated in *Craspedobolbina* (KESLING 1957b, Fig. 4) is based on the misinterpretation of a thin section cutting the cruminal opening far from the centre. It is possible that these structures are homologous with the thin membrane found in some cruminae of *Craspedobolbina* and the partition regularly occurring in *Apatobolbina*, formed in a similar way after the invasion of the crumina along the velum. It cannot be explained as being derived from the ventral wall of the valve, as the wall elements of all levels are still represented in the valve (cf. KESLING, op. cit., pp. 63–64).

(4) The fact that the crumina sometimes interrupts the velum and sometimes is more or less crossed by it is already explained (p. 107) as depending on the varying part taken by the velum in the inflation of the crumina in different forms. The velum did not grow across the crumina in different forms during the phylogeny (cf. KESLING, op. cit., pp. 64–66).

(5) The characteristic striation on the crumina, often like a finger-print pattern, marks parts of the crumina derived from the outside of the velum and possibly a narrow area along its base. Irregularities in the anteroventral region in the *Treposellinae* are rudiments of a phylogenetically earlier site of the female dimorphic characters (cf. KESLING, op. cit., pp. 66–67).

(6) There are clear phylogenetical trends showing a progressive enlargement of the crumina (*Craspedobolbininae*, *Treposellinae*, etc.), such as one might expect if these structures were developed for the purpose of accommodating the immature offspring. Though the appearance—but not the extinction—of the

forms exhibiting these trends must represent a chronological order for each branch in which such developmental trends are found, we can not, of course, expect to have found such a complete fossil record that we can use the evidence of chronological appearance as an argument against that of the phylogenetic analysis.

The primitive beyrichiacean and its ancestors

To summarize the evidence presented above and in the systematic descriptions, the lines leading back towards greater primitivity in the beyrichiids give us the following picture of the primitive beyrichiacean:

It was a palaeocope with an anterior lobe and a preadductorial knob. It had only one lobal feature behind the adductorial sulcus, the characteristic, broad syllobium. A zygal arch connected the preadductorial knob with the syllobium which also had a marked groove behind and slightly below the area of fusion with the zygal arch.

The marginal structures were fairly narrow, tubulous, and frill-like. The velum was broad, extending along all the ventral part of the valve, from the anterior to the posterior hinge corner. It was tubulous and frill-like. Anteroventrally it formed an almost globular or slightly oval crumina. The crumina was closed by a flap—not by fusion of its edge with the margin—and opened towards the domicilium by a secondary opening—not by a migration of a former dolonoid opening across the valve margin (cf. KESLING 1957b, pp. 70–71).

The ancestors of the beyrichiaceans were probably almost exactly similar to the primitive beyrichiaceans in lateral view. Their dolon was not necessarily lacking a radial tubulosity by expansion as is the case already in early stages of the dolonoid pouch in the beyrichiids; it is probable that the tubules continued unaltered across the dolon. The main difference was to be seen at the inner ventral side of the dolon where there was still an exterior opening, possibly partly covered by a folded flap from the edge of the dolon.

Though less certain and less important, there may have been some close similarities in ornamentation between the primitive *Beyrichiidae* and their ancestors. The primary pattern in the latter group was a granulosity, with a tendency towards reticulation; superimposed on it a faint verrucation or tuberculation could occur. At both sides of this critical point in the phylogeny, furthermore, the cristae occur, basically consisting of one ridge down the anterior lobe, one across the preadductorial knob, and two descending from the dorsal crest of the syllobium. The ventral junctions of these ridges, however, vary in the different forms having cristae (cf. p. 78). Finally, it is noteworthy that three different subfamilies develop a calcarine tubercle which seems to be homologous in all cases.

The morphological changes, then, at the point—or points—of origin of the *Beyrichiidae* were inconsiderable. The physiological changes, however, were obviously revolutionizing.

The functional interpretation

The fact just mentioned stresses again the lack of observations of soft parts and leads the discussion far beyond the fossil evidence. The interpretation can follow more than one line, and the possible alternatives and unverified details along these lines are overwhelmingly numerous.

Let us, however, for the sake of discussion, construct a plausible model of the development, starting from the presumptions that the change in the dimorphism followed functional lines and that the sex organs in these palaeocopes were partly or entirely situated in the hypodermis, with the uteri or even the uterine openings in the dolonal-cruminal region of the female:

Early ancestors of the *Beyrichiidae* had a slightly incurved dolon anteroventrally; in later phylogenetic stages it became pouch-shaped, and it gradually tended to close the dolonal opening by a flap. One of the explanations of this adaption is that it prevented eggs or even brood from falling out.

It is difficult to explain the following stage if the introduction of the eggs did not take place during the dolonal-cruminal metamorphosis. The eggs were introduced into the dolonal pouch and its opening was closed.

Probably at about the same stage a coil of the ovaries or uteri began to invade the velar fold by sinking into the enlarged portion of tubules during the metamorphosis, or by ejecting the eggs into it. This primitive cruminal space closed like the other tubules. Both the closed dolon and the closed crumina need a secondary opening in order to emit the brood. Such an opening could be established from the dolonal pouch by the penetration of one epithelial layer (Martinsson 1960b, Fig. 5C) during the metamorphosis; a similar opening from the cruminal pouch must penetrate two layers (Fig. 38C). The development had at this stage reached the level represented by *Craspedobolbina*.

In more advanced beyrichiids, as typically represented by the *Amphitoxotidinae*, the functionless dolonoid stage, which was still kept as an atavism in the ontogeny of *Craspedobolbina*, was abandoned. The closing of the cruminal space within the velum was probably abandoned later, and in the most advanced forms the eggs were then introduced directly into a primarily opening crumina.

This model cannot without serious hesitation be accepted as the hypothesis which the problem requires. Some of the major objections and alternatives within the scope of the fossil evidence will be given in the following discussion:

(1) The premise that the dolonal dimorphism had a function in reproduction has been regarded as incorrect by several authorities. A recent review of the literature on this problem was made by Jaanusson (1957, pp. 201–202). However, a structure specialized like the advanced velar dolon and following its developmental trends could hardly be non-functional.

(2) The premise that the uterine openings were anteroventral is sustained only by the location of the dimorphism in the fossil valves—in one not too distantly related palaeocope family, the *Primitiopsidae*, there is a closed posterior

dolonal pouch. It is also daring to assume that even such distal parts of the sex organs as the uteri could be located in the deeper part of hypodermis. This cannot be verified by any homologies in recent ostracodes. The conditions in the *Cyprididae*, in which the ovaries lie in the hypodermis, do not provide more than an indication of the possibility.

On the other hand, here, as in many other cases, it is dangerous to allege the presence or absence of conditions in the advanced *Podocopa* or *Myodocopa* as arguments for or against supposed conditions in the very specialized *Palaeocopa* which represent another, most probably blind, branch of the ostracode system. The specializations needed for the model above are by no means unreasonable with respect to other specializations in the sex organs of recent ostracodes. The dimorphic characters are, furthermore, situated just anteroventrally of that region round the adductorial sulcus where the space between the body and the hypodermis must be supposed to have been broadly bridged.

(3) If the slightly incurved dolon in a stage represented by, e.g., *Cystomatochilina*, served to attach the eggs in a secretion and was later, in a stage represented by *Chilobolbina*, developed into a pouch to shelter the eggs, only the thin epidermis of the inner layer of the velar fold need have separated the dolonal space and the uterine openings before the adult carapace was calcified. If the eggs were introduced into the dolon by penetration of this layer during the dolonal metamorphosis it would provide the logical explanation of how the external egg care could become an internal egg and brood care and why the dolonal tubules were engaged in this procedure. No traces of such openings have been recognized in dolonate ostracodes or in dolonoid beyrichiid stages, and the assumption lacks all empiric basis.

(4) We have no idea when the eggs were introduced into the dolonal and cruminal pouches, but even from a purely mechanical point of view the cruminal metamorphosis and in particular the inflation of the cruminal space are more easily explained if the egg mass took part in the procedure. Nor do we know at all when the copulation or fertilization took place, though it seems absurd to presume that the copulation took place before the secondary sexual characters exhibited in the dimorphism were developed. In that case, however, we have to make new unverified assumptions, viz. that the male copulatory organs or the seminal receptacles in the female were also adapted according to the changes from external to internal dimorphism.

(5) We do not know except by subjective analogy that the dolonal and cruminal pouches served the same purpose. Let us pick up from a discussion in earlier literature the assumption that the primitive dolon served to facilitate the copulation (Hessland 1949, p. 127) and assume that the dolonal pouch represents an advanced adaption for this purpose (e.g., a secretion vesicle or even a kind of seminal receptacle). If the fertilization took place in the anteroventral region, it is very probable that the egg and brood care, which was then a new feature in the *Beyrichiidae*, became located to this region. This alternative

avoids the difficulties in changing the transference of the eggs to the crumina instead of to the dolon—but how could the beyrichiids do without the former function of the dolon?

Only one investigation has been made of a large number of thin sections through closed dolonal pouches, and that was in the only family with an extreme posterior dolon, the *Primitiopsidae* (MARTINSSON 1956, p. 14). In 53 female specimens no traces of brood were found; egg care cannot be presumed to have left any traces. Alternatives like the last one cannot be entirely omitted from the discussion.

(6) The supposition that the metamorphosis has led to a perforation by rupture or resorption of a tissue layer before the eggs or brood became free is not particularly attractive. There are, however, enough analogies in the animal kingdom to such phenomena and those migrations of openings which the primary model above might imply.

Thus, however detailed the evidence may seem with the ontogenetic additions added in this study, the discussion of the functional adaptions during the development from a dolon to the crumina is still a manipulation with a wide range of unknown factors.

Notes on ecology, scavenger or parasite activity, and pathology

Some of the more noteworthy by-products of the morphological-systematical study are brought together here. Of these, particularly those associated with the ecology invite extensive study. Here only some general remarks, some of them with bearings on the taxionomical discussion, will be made.

The view generally held that the beyrichiids were benthic seems indisputable. To what extent they lived on or in the bottoms or in the phytocoenoses is not much known. In the few cases which have been checked a *Craspedobolbina* or *Beyrichia* species can occur in rocks representing a series of bottoms widely varying in muddiness. It is very probable, however, that they also lived to a great extent in the algal vegetation. In the beyrichiids, however, it is not so obvious as in some other ostracode groups that some faunal elements suddenly appear in samples which are not markedly different as to lithology and content of fossil remains from the zoocoenoses as compared with subcontemporaneous nearby samples. This is possibly a consequence of fluctuations in non-fossilized algal communities.

The beyrichiids were typically syngamic, and both sexes generally lived together in the same environment. They also generally lived all through the ontogeny in the same environment; in this respect they seem to differ from, e.g., the hollinids in the Silurian of Gotland.

Some research has been done as to the dynamics of beyrichiid "populations" (discussion in MARTINSSON 1955, pp. 12–17 and 1956 pp. 6–7; reference to an overlooked pioneer paper by SOHN 1950 should be added). The varying dura-

tion of the moult stages and the pseudocoenotic preservation of the arthropode shells, in combination with the three-dimensional character of the samples, make it very difficult to introduce true numbers and time factors in order to raise the discussion beyond an elementary descriptive stage. Simple histograms of the distribution of the extant fossils on growth stages show a more or less unevenly descending curve with its maximum in stage 8; stage 9, the first, is probably underrepresented (MARTINSSON 1956, Fig. 1).

In some instances a species of a beyrichiid genus may entirely dominate the fossil ostracode fauna, sometimes constituting 100 per cent of it, as *Craspedobolbina insulicola* on the *Ketophyllum* bottoms of Lerberget. But generally the beyrichiid populations are mixed with other palaeocope components in widely differing proportions, especially with primitiopsids and hollinids, and with smooth non-palaeocope ostracodes. Very often two or more species of a beyrichiid genus or of another palaeocope genus occur sympatrically. They are mostly so similar in size and carapace morphology that it is difficult to believe that they could have been adapted for different ecological niches.

A typical example is provided by the well analyzed Mulde fauna. The beyrichiids are here strongly dominated by one *Craspedobolbina* species; three closely related *Beyrichia* (*Beyrichia*) species occur as minor components. The primitiopsids are represented by one *Primitiopsis* and, at least, three very closely related *Clavofabella* species in roughly subequal proportions, and one *Leiocyamus* species as a minor component. There are numerous, but only adult, specimens of a *Triemilomatella* species and only extremely few specimens of another hollinid. In addition, there are some few unrevised palaeocopes and very numerous representatives of smooth non-palaeocope genera, among them *Thlipsurella*.

The sympatric occurrence of two very similar species can often be used as means of separating them.

It is common experience of the measurements that a very dominating species in an extreme and homogeneous environment shows far less size dispersion than species occupying a smaller place in the faunal pattern in a more varying matrix. The ontogenetic reconstructions based on material from Mulde have not yet been successfully repeated in other samples. The samples probably often consist of a mixture of minute chronodemes with different ecological characteristics leading to a strong size dispersion of a species in the total sample.

However, it is possible in several instances that samples of one species have been collected across two or more ecologically very different, thin chronodemes, each with a characteristic size distribution coupled with a characteristic range of lobal variation. Though the samples used in this study have been taken with the utmost care so as not to cross any stratigraphical boundaries, there is no guarantee that fairly different ecodemes have not been mixed. However large the material studied here may be, it is practically impossible to see through the false variational picture offered by such samples and avoid the creation of

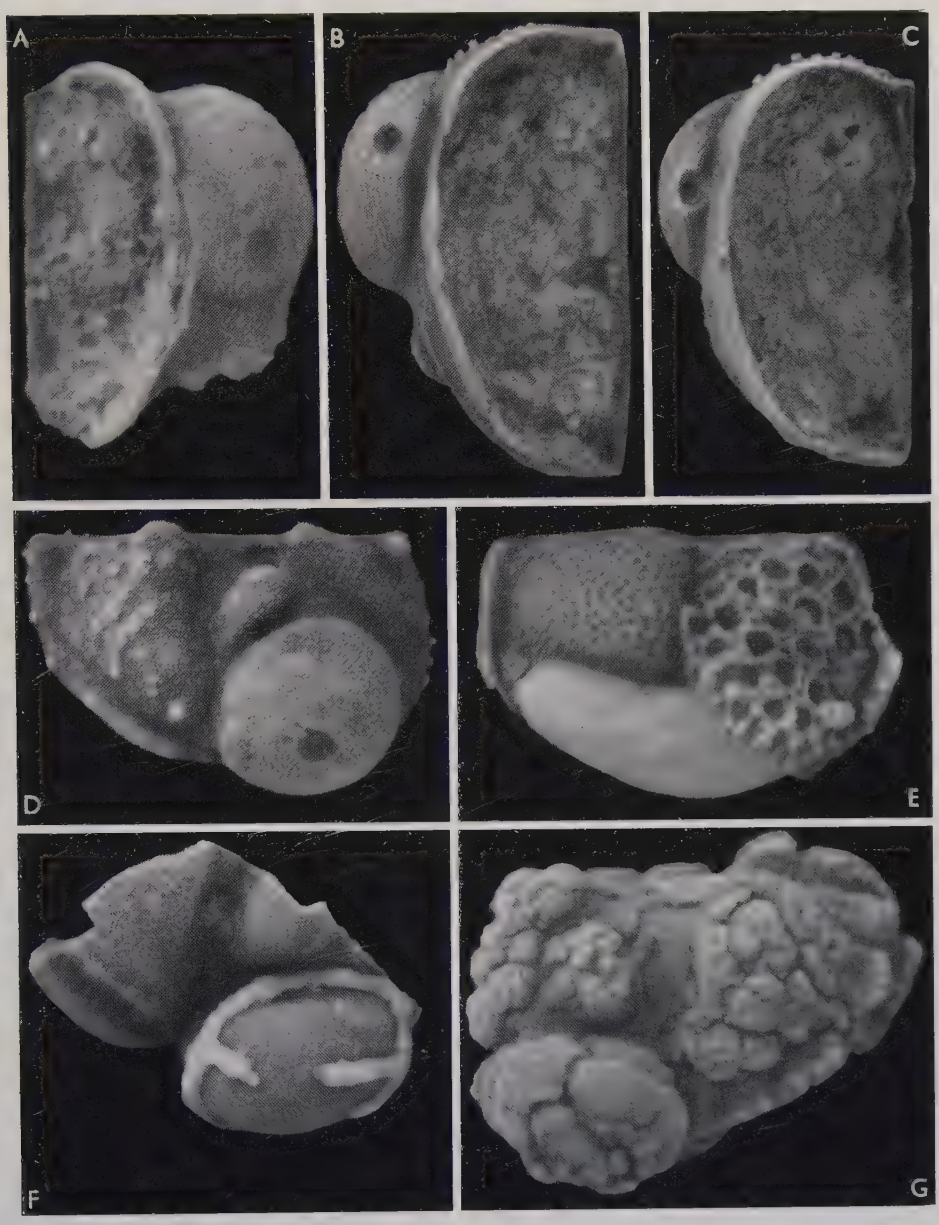


Fig. 40. Parasite or scavenger activity, epifauna, and pathology in beyrichiid ostracodes. A–D. The boring organism from Hammarudden. A. Boring in the crumina of *Hammariella pulchrivelata*, No. G 292. ×40. B. Same organism, crumina of *Neobeyrichia nutans*, No. G 293. ×30. C. Same organism, crumina of *Beyrichia globifera*, No. G 294. ×30. D. Same organism, crumina of *B. globifera*, No. G 295. ×30. E. Bryozoan growth on a right female valve, No. G 296, of *Clintiella hyrsiniana* from Hörsne. ×30. F. Fragment of a valve of *Craspedobolbina clavata* from Mulde with unknown growth on the crumina, No. G 297. ×30. G. Same species, same locality, No. G 298, a specimen showing a probably pathological dissolution and distortion of the carapace wall, resulting in a differentiation of the adductor muscle attachment. ×30.

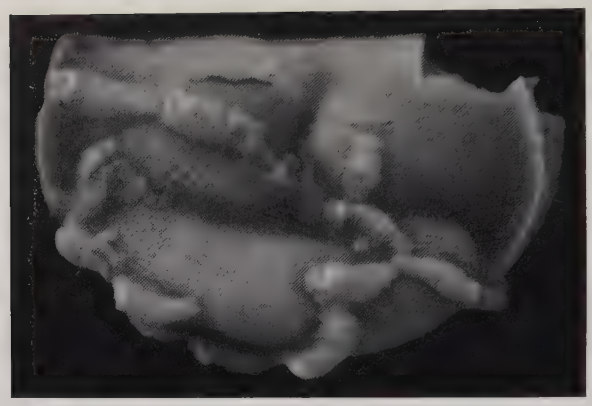


Fig. 41. Bryozoan growth on a female valve of *Clintiella* cf. *hyrsiniana* from Lau Backar. No. G 299. × 40.

typical morphospecies. A general norm in this respect has been not to complicate the taxionomy for possible future chronospecific revision based on large statistical materials from densely spaced localities. The "lumping" procedure has been preferred in such cases where the units distinguished cannot be judged with any certainty to be maintained at least as infra-specific taxia in practical work.

There are some environments in which other ostracodes were fairly abundant but where beyrichiids and other palaeocopes were rare or represented mainly by one very characteristic species. Such biotopes were many reef pockets and the bottoms covered by "*Sphaerocodium gotlandicum*". *Sleia equestris* seems to be very firmly associated with "*Sphaerocodium*" occurrences.

All kinds of pathological and teratological manifestations are extremely rare in the fossil parts of the beyrichiids. An interesting case is figured here (Fig. 40 G). The calcareous substance is distorted into a crumbled mass in which the lobes and the cruminae can be distinguished. The phenomenon seems to have spread concentrically from some points in the carapace, one of them especially distinctly developed on the right crumina. The velum is partly dissolved into irregularly papillose tubules. A feature of special interest is the flat elliptic area marking the place of the muscle attachment in the deeper part of the adductorial sulcus.

Traces of parasites or scavengers are also very rare. In some specimens furrows or other impressions, probably of jaws, have been observed, but it is mostly impossible to state if they were made during the life of the animal or after death. Borings in the carapace are also extremely rare, except for one thin marl layer represented in samples from Hammarudden where they are very common in all kinds of ostracodes present.

These holes seem to be fairly constant in diameter, about 100–130 μ, slightly tapering downwards. They are very often concentrated to the crumina and especially to its inner ventral part, in the striate part of it, if this kind of ornamentation is present. It is often associated with some shallow smaller pits

spread in one direction. The organism seems to have been specialized in ostracodes; other smaller shelly fossils in the samples have not been bored.

Growth on the shells of ostracodes is even rarer. Small bryozoan colonies have been recorded in a few cases (Figs. 40E and 41), and in *Craspedobolbina clavata* from Mulde an unknown organism growing on and branching across the crumina has been observed (Fig. 40F).

DESCRIPTIVE PART

Preparatory notes

When the "Treatise on Invertebrate Palaeontology", Part Q, Arthropoda 3, Crustacea, Ostracoda (Lawrence, Kansas, 1961) appeared, the present part could still be reworked, taking it into account. The views expressed in the Treatise on the carapace morphology and dimorphism in beyrichiids and other palaeocopes are so different from those presented in this study that it would be very difficult to insert comments and references in all the different places in the Introductory and General Parts where this would have been necessary. These comments have, however, been summarized in an Addendum (p. 355).

Some general remarks with bearing on the following systematic treatment will be made already here. It is stated that dimorphic structures are by far the most important criteria for palaeocope families (Scott 1961), but in the subsequent classification (Moore 1961) the taxia of family-group category cut across the groups characterized by homology of dimorphism. The classification proposed is largely based on Pokorný's classification as presented in 1958 (cf. Pokorný 1953) and has in common with it that the main units have been ranked one level higher than earlier. The *Kloedenellidae* and associated forms, however, regarded *incerti ordinis* by Pokorný, have been reintroduced as the suborder *Kloedenellocopina* into an order named *Palaeocopida* which also includes the suborder *Beyrichicopina* (=*Beyrichiida* Pokorný). As defined then, however, the *Kloedenellocopina* also comprise a series of other ostracodes ranging from genera with beyrichicopine characteristics (such as *Hallatia*, *Milleratia*, species referred to *Conchoprimitia*—such as *C. symmetrica*—and, possibly, *Pseudoleperditia* and *Tambovia*) to quite different forms recently referred to a new suborder, the *Eridostraca*, by Adamczak (1961, *Eridoconcha*, etc.).

In the units of the family-group category some re-groupings with direct bearing on the present study have been made. The *Beyrichiacea* are divided into two families after the distinction of two fundamentally different types of dimorphism, a *lobal* (=lobate) dimorphism in the *Zygobolbidae* and a *cruminal* (=beyrichiid) in the *Beyrichiidae* (Scott & Wainwright 1961). The *Eurychilinacea* of Jaanusson (1957) have been merged with the *Hollinacea* and his subfamilies *Chilobolbininae*, *Eurychilininae*, and *Piretellinae* have been

placed as families between, e.g., the *Hollinidae* and *Sigmoopsidae* which are regarded as having different dimorphic structures. To this must be remarked that the problems as to the homology of the dimorphic structures of the *Hollinacea sensu* JAANUSSON do not lie mainly within the superfamily itself but are connected with the homologization of the subhistial structure in *Carinobolbina*, *Sigmoopsis*, and associated genera on one side and the velum in non-hollinacean taxia on the other (cf. p. 88).

Non-beyrichiid families and superfamilies are mentioned in the present paper *sensu* JAANUSSON (1957), whose classification is based on the most thorough analyses hitherto of adventral structures and dimorphism through the palaeocope system. The separation of the *Primitiopsacea* in the Treatise seems, however, well founded (HESSLAND 1961). In the present paper the limitation of the *Palaeocopa* almost agrees with that of POKORNÝ (1953 and 1958), though largely from other points of view.

Finally some purely formal remarks on the new units in the Treatise must be added. The names *Beyrichicopina* and *Leperditicopida* are constructed by coordination of a generic name of Latin adjectival origin having the suffix *-ĭa* (fem. sing.) with the latinized Greek stem *cop-* and the Latin suffix *-īna* (neuter plur.). In such hybrid words (WIKÉN 1951, 226: 3a) there is always a connective vowel, *-o-*, between the Latin and Greek stems; it should be omitted only in pure Greek compounds like *Platycopa* (SARS 1866, p. 124; cf. WIKÉN 1951, 226: 1) where the first stem is an adjective with *-y-* before the ending. Latin adjectives in *-ĭus*, *-ĭa*, *-ĭum* are used in compounds without a connective vowel in one case, viz. in subordinations where they are followed by another Latin word (WIKÉN 1951, 226: 2a).

Though no rules exist as to the construction of order-group names, the Treatise "corrects" the old names constructed according to SARS by adding the endings *-ĭda* and *-īna* (cf. POKORNÝ 1953 and 1958) according to recent trends in taxionomy. It would be most unfortunate if it were to be compulsory to use the same suffixes in the neuter plural (*-ida*, *-ina*) in order-group names and in masculine (sic!) and feminine plural (*-idae* and *-inae*, respectively) in family-group names. In those frequent cases when these names are anglicized, scandinavianized, or germanized in current text, this has as a consequence that order and suborder names become identical (*beyrichiids*, *beyrichiider*, and *Beyrichiiden*, respectively, for both *Beyrichiidae* MATTHEW and *Beyrichiida* POKORNÝ; suborders and subfamilies accordingly). Below *Leperditiocopa* will be used for *Leperditicopida* SCOTT (*Leperditiida* POKORNÝ).

In the synonymy lists below only essential taxionomic key references have as a rule been included; *partim*, *confer*, and *non* references have been used very restrictively; they are largely covered by extant index papers (cf. p. 360).

Shortness will also characterize the descriptions following the diagnoses where repetitions of diagnostic characters are avoided as far as this is technically or stylistically possible.

There seems to be no reasonably consistent method of expressing the relative abundance of the different species; only when the material behind the descriptions is remarkably limited has this been stated under "Occurrence".

Palaeozoic straight-hinged ostracodes. The delimitation of the Palaeocopa and the systematic position of the Beyrichiidae

The classification of the *Palaeocopa* as presented in the Treatise, which will certainly be used all over the world as the standard handbook in ostracodology, is not in agreement with the classificatory principles to be derived from the morphological discussion presented above. The place of the *Beyrichiidae* among the palaeozoic straight-hinged ostracodes—a group of ostracodes whose interrelations are far from clear—is illustrated in the following classification which will be further discussed below.

Order	*Ostracoda* LATREILLE 1802 [*nom. correct.* LATREILLE 1806]
Suborder	*Palaeocopa* HENNINGSMOEN 1953 [*nom. correct.* JAANUSSON 1957, restricted herein]
Superfamily	*Eurychilinacea* ULRICH & BASSLER 1923 [*nom. transl.* JAANUSSON 1957, restricted]
Superfamily	*Beyrichiacea* MATTHEW 1886 [*nom. transl.* ULRICH & BASSLER 1923]
Superfamily	*Primitiopsacea* SWARTZ 1936 [*nom. transl.* HESSLAND 1961]
Superfamily	*Hollinacea* SWARTZ 1936 [*nom. transl.* JAANUSSON 1957]
Superfamily	? *Kirkbyacea* ULRICH & BASSLER 1923 [*nom. transl.* JAANUSSON 1957]
Superfamily	? *Leperditellacea* ULRICH & BASSLER 1923 [*nom. transl.* JAANUSSON 1957]
Suborder	*Leperditiocopa* POKORNÝ 1953
Suborder	*Kloedenellocopa* SCOTT 1961 [restricted]

The *Archaeocopida* SYLVESTER-BRADLEY and the *Eridostraca* ADAMCZAK are left out of consideration as not affecting the problems treated here.

Palaeocopa

DIAGNOSIS.—Small to medium-sized, exceptionally large, ostracodes with a long, straight hinge and a preplete or amplete, occasionally slightly postplete, outline. Lobation consisting of, associated with, or derivable from the following main elements: *A preadductorial node in front of a marked adductorial sulcus*, one anterior lobe in front of the preadductorial node, and one or two lobes behind the adductorial sulcus. *Adventral marginal and supramarginal structures* present or reduced; the supramarginal structures—velum and histium—may exhibit a *sexual dimorphism, always associated with the formation of a dolon.* Carapace without traces of a circulatory system.

REMARKS.—In several forms one or more of the diagnostic characters may be missing (e.g. *Apatobolbina*, tecnomorphs of the *Leiocyaminae*, etc.) or so strongly specialized that they are not readily recognized (e.g. genera of the *Treposellinae*), but they are then firmly connected by other homologies with the typical forms. Such homology systems are easily recognized within the four first superfamilies mentioned in the scheme above; in the *Kirkbyacea* the lobal homologies are somewhat obscure and the dimorphism absent, but the general morphology

of the adventral structures is regarded as a strong argument for their inclusion in the *Palaeocopa*. The *Leperditellacea* need a thorough revision before their place in the classification can be definitely established, as further discussed below (p. 129).

Eurychilinacea

DIAGNOSIS.—*Palaeocopa* with anterior, anteroventral, or almost medioventral dimorphic characters exhibited by a velar dolon.

REMARKS.—The restriction of the family as compared with earlier diagnosis (JAANUSSON 1957, p. 228) consists in the separation of the *Primitiopsidae* from this superfamily. The *Aparchitidae* must be placed among *Palaeocopa incertae sedis* until a revision of the *Aparchites* problem has been made. The absence or lack of recognition of dimorphic characters in some *Quadrijugatorinae* does not seem to necessitate a reservation in the diagnosis.

Beyrichiacea

DIAGNOSIS.—*Palaeocopa* with cruminal dimorphism.

REMARKS.—The phylogenetic relationships with the dolonate superfamilies are evident from the discussion in the General Part. A series of *Zygobolbinae*, regarded by SCOTT & WAINWRIGHT (1961) as exhibiting a lobal dimorphism, is still entirely uninvestigated as to the origin of the dimorphic pouch or swelling in the carapace. The assumption that even the extreme cases of zygobolbine pouches have originated by incorporation of valve elements with the originally velar crumina, resulting in a minor displacement of it, seems, however, to be tenable in all cases.

Primitiopsacea

DIAGNOSIS.—*Palaeocopa* with posterior or markedly posteroventral dimorphic characters exhibited by a velar dolon.

REMARKS.—The phylogenetic aspects of the dimorphism in the *Beyrichiidae* presented above show that the trends towards a specialization of the anteroventral dolon led to the branching off of the cruminal line not long before the dolon reached its maximum development. Another group of palaeocopes followed extremely opposite trends culminating in the formation of an extremely posterior, closed dolonal pouch. The morphological discontinuity is considerable; though the *Primitiopsacea* show clear relationships with the *Eurychilinacea* there are no forms known at present which can be regarded as really transitional. The physiological consequences of this specialization are unknown. In order to illustrate the main branches of development within the *Palaeocopa* the primitiopsid branch has to be regarded as a unit of at least the same rank as the *Eurychilinacea*.

The development in the *Primitiopsinae* also shows a pronounced trend towards the incorporation of wall elements with the pouch, but the pouch remains clearly dolonal in the most advanced forms contained in the undescribed material from Gotland.

Hollinacea

Remarks.—Reference is made to Jaanusson's (1957, p. 375) diagnosis and to the discussions of the hollinacean dimorphism above (p. 88).

Kirkbyacea

Diagnosis.—*Palaeocopa* with more or less typical, non-dimorphic velum. Lobation strongly specialized, typically consisting in more or less sharp longitudinal plications which even cross the sulcal region; sulcal features typically reduced to a ventromedian pit or unornamented spot. Surface reticulate.

Remarks.—The association of kirkbyacean lobal features with the general lobal pattern of the *Palaeocopa* meets with some difficulties. In such genera as *Kellettina*, *Kindlella*, *Polytylites*, and *Kegelites* (cf. especially Sohn 1954), the derivation seems possible. The far-reaching similarity in the morphology of the adventral structures is regarded as a tenable argument for the association of this superfamily with the more typical *Palaeocopa*.

Leperditellacea

Remarks.—This superfamily, *sensu* Jaanusson (1957), still comprises ostracodes in which the lobal characteristics, and probably even adventral structures, may possibly be derived from the palaeocope pattern, such as the bolliines and ulrichiines (*N.B.* the exclusion of the *Neodrepanellinae* Zaspelova 1952). The type genus, however, seems to be very similar to *Conchoprimitia* which has a strikingly leperditioid carapace with traces of a circulatory system like that of the *Leperditiocopa*. According to the views on the limitation of the *Palaeocopa* expressed here, this and related genera should most likely be regarded as leperditiocopes. They seem to lack important leperditiocope characteristics, such as the stratification of the shell and the denticulate hinge. These may, however, like the advanced circulatory system, possibly be a function of the large size of most *Leperditiocopa*. Investigations are lacking as to this point.

Leperditiocopa

Diagnosis.—Large to very large ostracodes with straight hinge and postplete outline, lacking adventral and major lobal structures. Muscle scars strongly differentiated into a major adductorial group and minor groups; traces of a radiating lacunar system occur in the adductorial region.

Remarks.—Like the *Palaeocopa*, most *Leperditiocopa* have a node in front

of or above the adductorial region, the "eye tubercle" of many writers; it is, however, premature to suggest any homology of this node with the most persistent feature in the palaeocope lobation, the preadductorial node.

Kloedenellocopa

DIAGNOSIS.—Straight-hinged ostracodes without supramarginal adventral structures; dimorphism, if detectible, occurs through posterior inflation of the rear part of the female carapace; lobal structures with an adductorial sulcus as the most persistent feature.

REMARKS.—Forms with lobal and adventral structures among the *Beyrichiopsidae*, as represented in the Treatise by *Beyrichiopsis fortis* and "*Tambovia*" *sculpta*, should be excluded from the *Kloedenellocopa* according to the diagnosis and be placed as *Palaeocopa incertae sedis*. As figured by POLENOVA (1952) there is a swelling in the posterior part of the carapace of one specimen which might be interpreted as a kloedenellacean dimorphism; a revisional investigation of this phenomenon should be made.

The kloedenellocopes develop a sulcation and lobation which superficially might seem very similar to the conditions in the palaeocopes (cf. HENNINGSMOEN 1953, Fig. 3); there are maximally four lobes and three sulci. However, there are no detectible homologies except for the adductorial sulcus; there is no defined preadductorial node or any detectable genetic relationship as to the other sulci.

The words "straight-hinged" or "straight-backed" are not fully adequate as diagnostic terms, as the former term can be applied to hinges in representatives of most major ostracode groups and the latter is inadequate for many dorsate ostracodes with a straight, long hinge. The expressions are, however, so deeply founded in traditional usage that they hardly lead to confusion.

Generic characters of the Beyrichiidae

The subfamilies of the *Beyrichiidae* are based on the main branches in the development of dimorphism as discussed in the General Part. However, these branches or trends are not continuously verified in the fossil record, and the major discontinuities or apparent leaps and bounds in the development have generally been used as genus boundaries.

This method generally functions well, is tenable from the point of view of neontological systematics, and is mostly corroborated by differentiations or discontinuous trends in the development of lobal and ornamental characters. In the *Craspedobolbininae* and the *Beyrichiinae* qualitatively less considerable discontinuities or developmental trends have been used for a division into subgenera.

In the *Amphitoxotidinae* a generic classification solely based on developmental

trends in the cruminal morphology is not tenable; it does not correlate with trends in the development of the lobation. It is evident that considerable variations in the inflation of the crumina take place along similar lines within groups corresponding to genera in the other subfamilies. The generic grouping in this family is, therefore, largely founded on trends and discontinuities in the morphology of the lobal structures and non-dimorphic parts of the adventral structures.

Such general beyrichiid features as the outline and normal smaller variations in the lobation and in the adventral structures, which are described in the General Part and are immediately and better comprehended from the figures than from a lengthy verbal description, will not receive further attention below.

Family BEYRICHIIDAE Matthew 1886

[*nom. transl. et correct.* Miller 1889, p. 523,
e Beyrichinae Matthew 1886]

Diagnosis.—Identical with the diagnosis of the superfamily *Beyrichiacea*, p. 128.

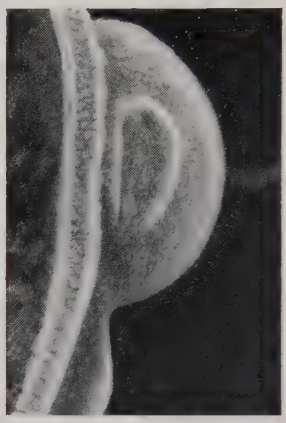
Subfamilies.—*Craspedobolbininae* n.subf.
Treposellinae Henningsmoen 1954
Amphitoxotidinae n.subf.
Zygobolbinae Ulrich & Bassler 1923
Beyrichiinae Matthew 1886
Kloedeniinae Ulrich & Bassler 1923
Hexophthalmoidinae n.subf.

Remarks.—Though the subfamilies represent widely different degrees of specialization, they have all been regarded as subfamilies, as all of them represent well established developmental lines leading back to a similar origin of the crumina.

An exception to this are the *Hexophthalmoidinae*, an apparently very aberrant group represented only by one species, and the genus *Kolmodinia* which is placed *incertae sedis*. If any of the other groups, except possibly the practically unrevised *Kloedeniinae*, were assumed to be translated into a family this would result in the breaking up of the family into at least five beyrichiacean families (in an extreme case only the *Craspedobolbininae* and *Amphitoxotidinae* could be kept together as subfamilies of a common family). This operation would probably be in agreement with the current inflation in taxionomic rank in fossil ostracodes, but it is not to be recommended to carry it out without a revision of the *Kloedeniinae* and an analysis of the many unrevised zygobolbine genera.

Subfamily *Craspedobolbininae* n. subf.

Diagnosis.—*Beyrichiidae* with cruminal metamorphosis passing a complete dolonoid stage, implying a completed closing off of the dolonoid space by a flap.



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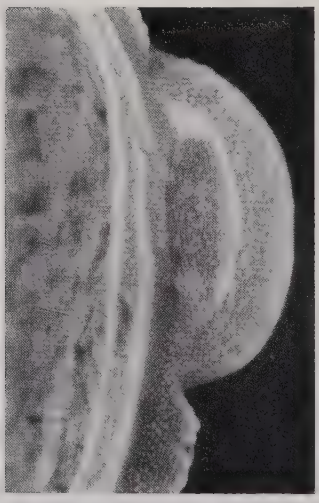

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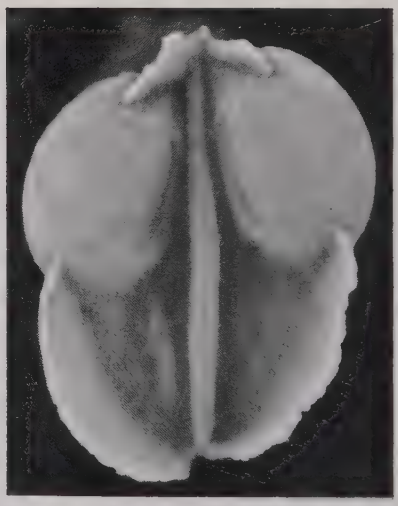

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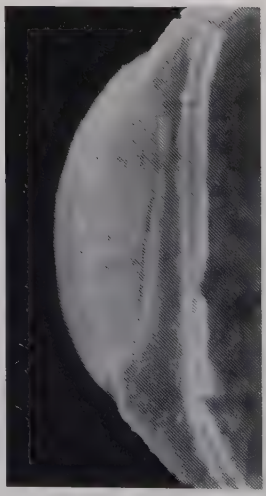
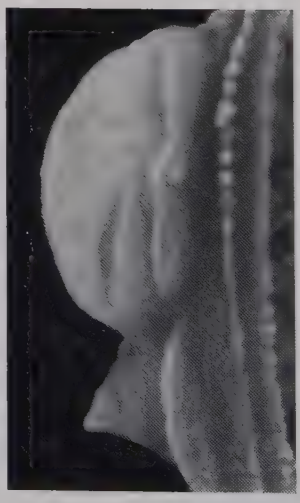




TYPE GENUS.—*Craspedobolbina* KUMMEROW 1924

GENERA.—*Apatobolbina* ULRICH & BASSLER 1923
Leptobolbina n.g.
Bolbibollia ULRICH & BASSLER 1923
Bolbineossia KESLING, HEANY, KAUFMANN & ODEN 1958
Craspedobolbina KUMMEROW 1924
Hyrsinobolbina n.g.
Aitilia n.g.
Hamulonavis n.g.
Mesomphalus ULRICH & BASSLER 1913
Clintiella n.g.
Barymetopon n.g.

REMARKS.—A survey of the ventral morphology in representative *Craspedobolbininae* is shown in Fig. 42 together with the most primitive amphitoxotidine, *Sleia equestris* (Fig. 42: 8).

Within the *Apatobolbina–Leptobolbina* group there is a pronounced, definitely homoeomorphic, trend towards the simplification of the cruminal metamorphosis realized in the *Amphitoxotidinae*.

There are trends towards the reduction of the broad velum into a velar ridge (*Aitilia*, *Mesomphalus*). The reduction of the lobal features leads in one branch to the total obsoletion of lobation (*Apatobolbina*); in others it reaches a stage where practically only the very persistent adductorial node and preadductorial sulcus are present (*Hamulinavis*, etc.). In the ornamentation there are tendencies towards a well-developed reticulation (*Bolbineossia*), more or less successfully realized in other genera (*Mesomphalus*, etc.).

Bolbibollia and *Leptobolbina* are among the smallest beyrichiid genera; the other genera can be characterized as medium-sized.

OCCURRENCE.—Silurian of Europe and eastern North America. One genus, *Mesomphalus*, reaches into the Devonian of Maryland. In the sequence of Gotland the last craspedobolbinines occur in the basal parts of the Eke Beds (Lau Backar).

Genus *Apatobolbina* ULRICH & BASSLER 1923

DIAGNOSIS.—Granulose *Craspedobolbininae* with completely obsolete lobation and a broad, tubulous velum forming a globular crumina. Velar margins do not reach into the dolonoid scar; no ridge below the scar.

Fig. 42 (opposite page, cf. MARTINSSON 1960 b, Plate IV). Ventral morphology of the crumina in the subfamily *Craspedobolbininae* (1–7) and in a primitive representative of the *Amphitoxotidinae* (8). 42:1. *Craspedobolbina* (*Clavobolbina*) *acuminulata* n.sp., Slite Beds, Follingbo I. ×45. No. G 220. 42:2–3. *Craspedobolbina* (*Mitrobeyrichia*) *variolata* n.sp., Slite Beds, Svarvare. ×45. Nos. G 208 and G 221, respectively (locality previously named Klinte, MARTINSSON, op. cit.). 42:4. *Craspedobolbina* (*Mitrobeyrichia*) *unculifera* n.sp., Högklint Beds, Visby I. ×45. No. G 222. 42:5. *Apatobolbina simplicidorsata* n.sp., Lower Visby Beds, Nyhamn (parish of Lummelunda). ×45. No. G 223. 42:6. *Apatobolbina gutnica* n.sp., Högklint Beds, Visby I. ×45. No. G 224. 42:7. *Clintiella* cf. *hyrsiniana*, Eke Beds, Lau Backar. ×45. No. G 225. 42:8. *Sleia equestris* n.sp., Eke Beds, Lingvide (parish of Grötlingbo). ×45. No. G 226.

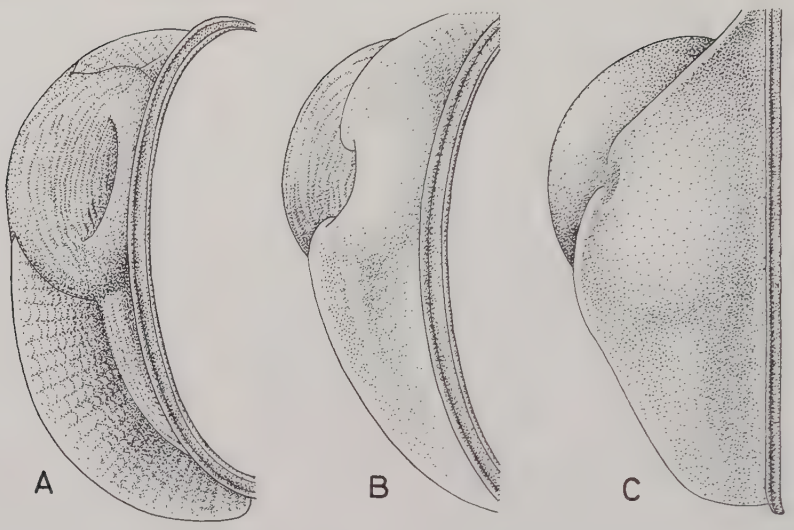


Fig. 43. Ventral morphology of the crumina and the velum in *Apatobolbina* and *Leptobolbina*. A. Based on *Apatobolbina gutnica* n.sp. B. Based on *Leptobolbina hypnodes* n.sp. C. Based on *Leptobolbina quadricuspidata* n.sp. A ×45. B ×75. C ×80.

Type Species.—*Apatobolbina granifera* Ulrich & Bassler 1923, by original designation.

Species.—*Apatobolbina platygaster* Kummerow 1924
Apatobolbina granifera Ulrich & Bassler 1923
Apatobolbina michiganensis n.sp.
Apatobolbina simplicidorsata n.sp.
Apatobolbina gutnica n.sp.
Apatobolbina tricuspidata n.sp.

Remarks.—*Apatobolbina acuta* Ulrich & Bassler 1923 is a *nomen nudum*; in the literature (Ulrich & Bassler 1923, Bassler 1927) there has been no confirmation that dimorphism has been observed in this species.

Occurrence.—Silurian of Baltoscandia and North America (Anticosti Island, Pennsylvania, and Michigan). In the sequence of Gotland the genus occurs from the oldest strata exposed to the lowermost part of the Högklint Beds.

Apatobolbina platygaster Kummerow 1924

1924 *Apatobolbina platygaster* n.sp.—Kummerow, p. 428; Pl. 20 (numbered 21), figs. 29–31.

Remarks.—*A. platygaster* differs, according to Kummerow's illustrations (l.c.), from all other species of *Apatobolbina* examined (but not from the reconstruction of *A. granifera* by Ulrich & Bassler 1923) by having an uninterrupted velum along all the non-dorsal part of the outline, and by a small dorsal ridge

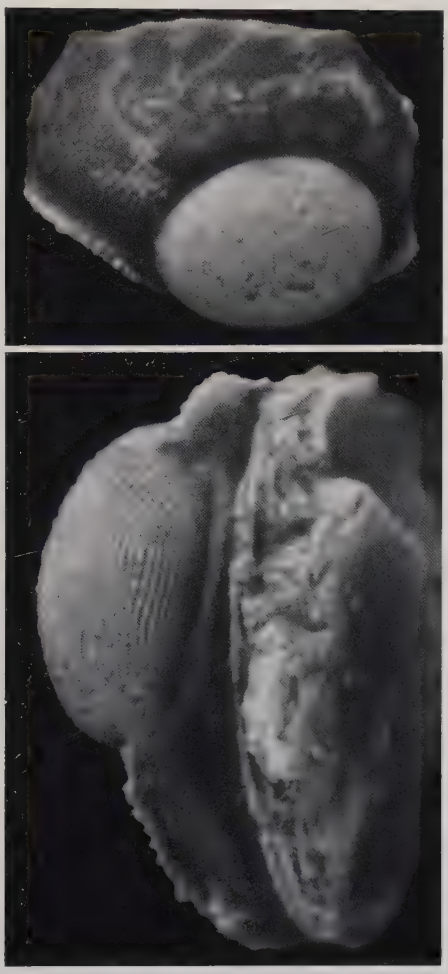


Fig. 44 A. *Apatobolbina* cf. *granifera* ULRICH & BASSLER 1923, Jupiter River Formation, East Jupiter Cliff, Anticosti, Quebec, Canada. ×40. No. NA 72.

Fig. 44 B. Same specimen, ventral view; anterior end up. ×60.

The American *Apatobolbina* species, especially *A. michiganensis*, differ from their European relatives by the short distance between the ends of the unspecialized portions of the velum; cf. Fig. 43 A on opposite page.

on the syllobium near the posterior corner. The reliability of the drawings can, with knowledge of other forms figured in the same paper, be questioned. The originals are not to be found among KUMMEROW's originals returned by the U.S.S.R. to the Berlin museums.

Apatobolbina granifera ULRICH & BASSLER 1923

1923 *Apatobolbina granifera* n.sp.—ULRICH & BASSLER, p. 522; Pl. XXXVII, figs. 17–19; Fig. 16: 6.

REMARKS.—The reconstruction of the velum by ULRICH & BASSLER does not agree well with photographical figures which show tecnomorphic valves with a posteriorly restricted velum. Specimens from the Anticosti occurrence referred to by ULRICH & BASSLER (1923, p. 523) have been examined for this

study (Fig. 44) and show a restricted velum. The Anticosti species differs from all closely related European species by the very short distance between the remaining parts of the velar edge and the dolonoid scar, and by the evenly convex dorsal ridge. The velum has probably been considerably narrower than in any European species known.

Apatobolbina michiganensis n.sp.

1957 *Apatobolbina* sp.—Kesling & Rogers, p. 999; Pl. 129, figs. 8–11.

Derivation of the Name.—Lat. *Michiganensis*, from the State of Michigan.

Holotype.—A left female valve, Mus. Pal. Univ. Michigan No. 30492 (Kesling & Rogers, op. cit., Pl. 129, figs. 8–9).

Type Occurrence.—Schoolcraft Formation, Middle Silurian of Michigan.

Diagnosis.—*Apatobolbina* with the posteroventral portion of the velar edge reaching immediately behind the posterior end of the dolonoid scar, not encroaching onto the crumina.

Description.—No lobal characters except a flattened dorsum which protrudes slightly over the hingeline, reaching its highest point about $\frac{1}{4}$ of the hinge length from the posterior corner where it bends down gently in posteroventral direction. A slight depression in the adductorial region may be present. Velum restricted at a point vertically below the posterior hinge corner, broad, tubulous. Crumina suboval, the posterior end of the dolonoid scar, at least, is inconsiderably separated from the velar edge which does not encroach onto the crumina (Kesling & Rogers, op. cit., Pl. 129, Fig. 9). Surface sparsely granulose, especially lateroventrally; crumina with the typical *Apatobolbina* striation (see Figures, op. cit.).

Remarks.—The construction of the crumina, which is the most primitive of those observed in the genus, distinguishes *A. michiganensis* from all other *Apatobolbina* species.

Apatobolbina simplicidorsata n.sp.

Figs. 42: 5 and 45.

Derivation of the Name.—Latin *simplex* (stem *simplici-*) simple, and *dorsatus*, provided with a dorsum.

Holotype.—A left female valve, No. G 300 (Fig. 45 A).

Type Stratum and Locality.—Lower Visby Beds at Nyhamn, Gotland.

Diagnosis.—*Apatobolbina* with dolonoid scar widely separated from the unmetamorphosed parts of the velum which encroach on the crumina. Velum restricted at the rearmost part of the crumina. The simple dorsum makes a distinct bend about one third of the hinge length from the posterior corner.

Description.—Except for the dorsum (see diagnosis) the only lobal-sulcal feature is the external muscle spot. The restricted velum (see diagnosis) is

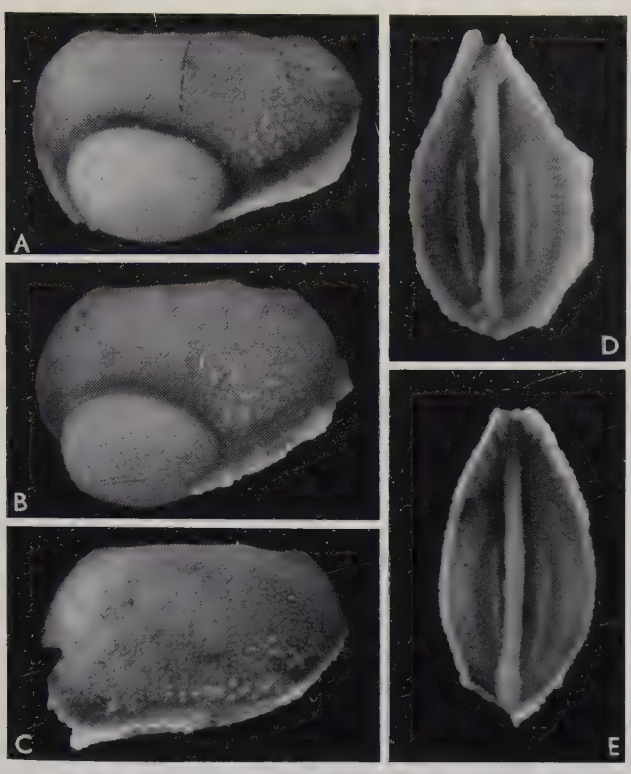


Fig. 45. *Apatobolbina simplicidorsata* n.sp., Lower Visby Beds, Nyhamn. ×30. A–B. Female valves, Nos. G 300 (holotype) and G 301. C. Male valve, No. G 302. D–E. Ventral view of tecnomorphic carapaces (anterior end up), Nos. G 303 and G 304.

tubulous, rather broad, extending from the foremost to the rearmost points of the carapace and is broadest anteroventrally. Crumina suboval (see further diagnosis), striate. Low striate toric ridge along the margin. Surface almost smooth along the hingeline; a granulose pattern increases in density and coarseness towards the base of the velum (Fig. 45).

Dimensions.—Hinge length 800–1000 μ, adductorial height 740–1030 μ (see size dispersion of 27 female specimens in Fig. 48).

Remarks.—This species has a cruminal morphology which is very similar to that of *A. gutnica* but differs from it by the shape of the dorsum, the site of the toric ridge in the tecnomorphs, and slightly in the width of the velum (this is not well illustrated, as the velum usually breaks away more frequently in *A. simplicidorsata*). As in the other *Apatobolbina* species, the delicate flange-like marginal structures and the contact conditions of the valves have not been studied in detail.

Occurrence.—Gotland, exclusively in the Lower Visby Beds: Nyhamn, Nyhamn well, Gustavsvik, Buske.

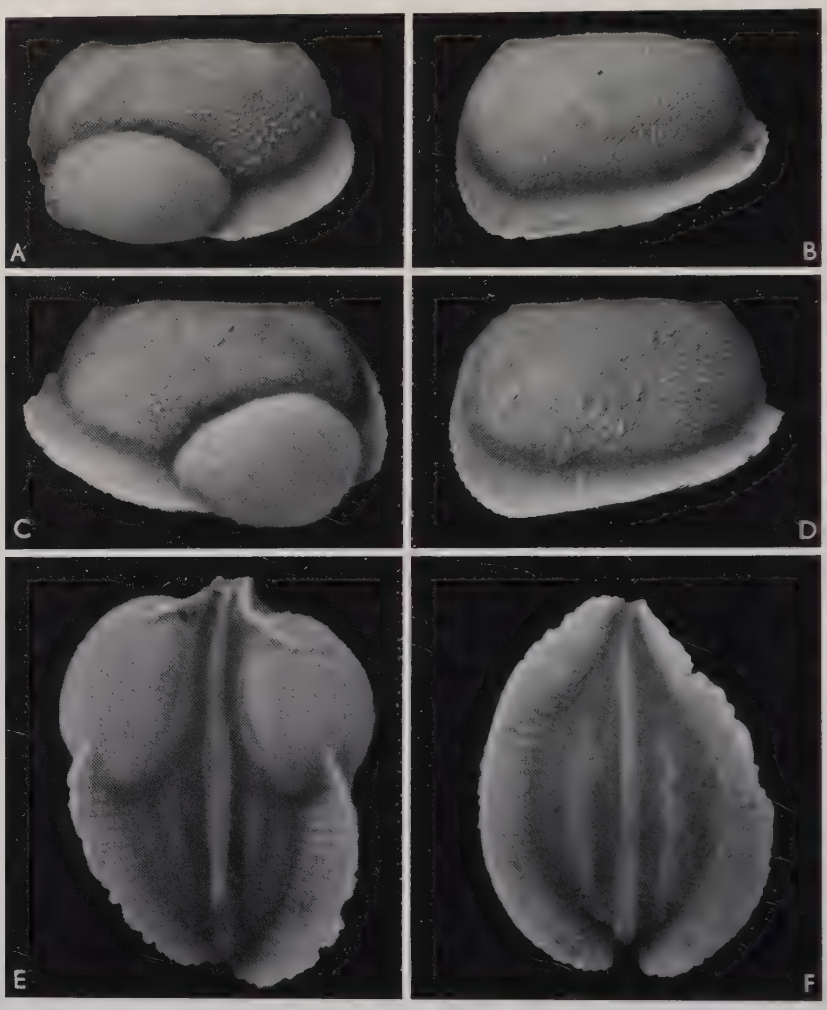


Fig. 46. *Apatobolbina gutnica* n.sp., Högklint Beds, Visby I. A–D. Female valves (left) and male valves (right) in lateral view. ×30. E–F. Female and male carapaces in ventral view, anterior end up. ×40. A. No. G 305 (holotype). B. No. G 306. C. No. G 307. D. No. G 308. E. No. G 309. F. No. G 310.

Apatobolbina gutnica n.sp.

Figs. 35A, 42: 6, 43A, and 46.

Derivation of the Name.—Latinized adjective *Gutnicus*, associated with the people (or language) of Gotland.

Holotype.—A left female valve, No. G 305 (Fig. 46A).

Type Stratum and Type Locality.—Lowermost Högklint Beds at Visby I, Gotland.

Diagnosis.—*Apatobolbina* with dolonoid scar widely separated from the

unmetamorphosed portions of the velum which encroach on the crumina. Velum very broad up to the constriction at the rearmost point of the carapace. Rear part of the dorsum not protruding much over the hingeline, nor making a distinct bend.

Description.—For dorsum, see diagnosis. Muscle spot very distinct even in the female. The velum begins at the foremost point of the carapace, widens gently along its anteroventral portion and almost keeps its maximal width upto its rounded constriction at the rearmost point of the carapace. The dolonoid scar of the crumina is generally much nearer the edge of the anterior unmetamorphosed part of the velum than to the posterior. The membraneous partition in the cruminal opening has been observed in several specimens of this species (Fig. 35A). In the dark field inside the base of the velum in the subvelar field of the tecnomorphs, the low striate toric ridge is situated about half-way between the margin of the valve and the margin of the dark area. Surface of the valve almost smooth anterodorsally, increasingly granulose in posterior and ventral direction. Crumina striate (Fig. 42:6).

Remarks.—The differences between *A. gutnica* and *A. simplicidorsata* are stated under the latter species. A closely related, unrevised species has been recorded from Norway (*A. platygaster*, cf. Henningsmoen 1954).

Dimensions.—Hinge length – adductorial height of ten female specimens from the type locality (valves of both sides, measures in microns):

1120 – 1025, 1065 – 1010, 1065 – 945, 1045 – 965, 1010 – 970, 990 - 960, 980 – 910, 965 – 100, 960 – 950, 890 – 900.

The valves are often compressed. See also the size dispersion diagram, Fig. 75.

Occurrence.—Gotland, exclusively in the lower parts of the Högklint Beds: Visby I, Lickershamn II. A damaged specimen possibly belonging to this species, from the Upper Visby Beds at Ygne, has not been definitely determined.

Apatobolbina tricuspidata n.sp.

Fig. 47.

Derivation of the Name.—Latin *tres*, three, and *cuspidatus*, provided with cusps.

Holotype.—A left female valve, No G 312 (Fig. 47B).

Type Stratum and Type Locality.—Upper Visby Beds at Gnisvärd, Gotland.

Diagnosis.—*Apatobolbina* with the remaining parts of the velar edge widely separated from the dolonoid scar. Three dorsal cusps near the hinge protrude over the hingeline.

Description.—Lobal features consisting only of the faintly marked, cusp-bearing dorsal ridge (see diagnosis). The adductor muscle spot is not always distinctly marked. Velum broad, tubulous, extending from the foremost to the

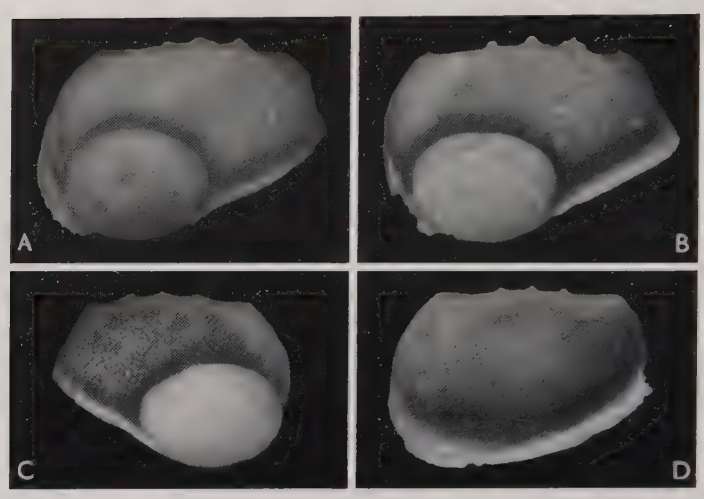


Fig. 47. *Apatobolbina tricuspidata* n.sp., Upper Visby Beds. ×30. A. Female valve from Halls Huk, No. G 311. B. Female valve from Gnisvärd (holotype), No. G 312. C. Small female valve from Halls Huk, No. G 313. D. Tecnomorph from Halls Huk, No. G 314.

hindmost point of the valve. Crumina striate, closing mechanism similar to that in the two preceding species. Low striate toric ridge relatively near to the ventral margin. Material from the southern part of the distribution area almost smooth in the adductorial region, with rather scattered coarse granules in the preadductorial half of the valve, in a finer granulose ground pattern which may also cover the anterodorsal part of the valve. Some specimens from Halls Huk more evenly granulose, pattern coarser and denser in posteroventral direction (Fig. 47).

Dimensions.—Hinge length–adductorial height of ten right and left valves from the type locality (measures in microns):

990–840, 965–920, 965–905, 965–890, 960–930, 950–880, 940–920, 885–830, 870–850, 830–865.

Five specimens from Halls Huk:

1000–985, 950–940, 870–60, 800–630, 780–725.

The first two specimens had the normal ornamentation, the other three were more evenly granulose; probably the sample has cut through an ecodeme with smaller average size.

Remarks.—The three cusps—the number very rarely varies—are diagnostics excluding all other known species. The species, however, varies more than the other *Apatobolbina* species described above, as already seen from the few specimens figured; this is true for both size and ornamentation.

Occurrence.—Gotland, exclusively in the Upper Visby Beds: Halls Huk, Irevik I, Snäckgärdsbaden, Gnisvärd.

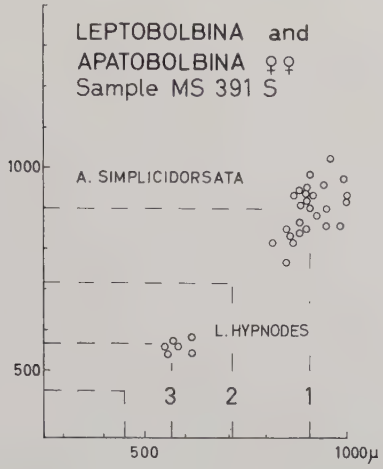


Fig. 48. Size dispersion of female specimens of *Apatobolbina simplicidorsata* and *Leptobolbina hypnodes* n.sp., in the Lower Visby Beds at Nyhamn. Dashed lines refer to moult rates of *Apatobolbina simplicidorsata* (hinge length against sulcal height).

Genus *Leptobolbina* n.g.

Fig. 49.

Derivation of the Name.—Latinized Greek *lepto-*, thin (referring to the shape of the velum), and the generic name *Bolbina*, frequently used in names of beyrichiid genera.

Type Species.—*Leptobolbina quadricuspidata* n.sp.

Species.—*Leptobolbina hypnodes* n.sp.

Leptobolbina quadricuspidata n.sp.

Diagnosis.—Small *Craspedobolbininae* without any lobation or with only the cusp of the anterior lobe. Crumina formed *via* the closing of a very small, abmarginally situated dolonoid pouch; the edge of the velum continues into the dolonoid scar.

Fig. 49. *Leptobolbina* n.g. Drawing based on *Leptobolbina quadricuspidata* n.sp., ×60.

Fig. 50. *Leptobolbina hypnodes* n.sp., Lower Visby Beds, Nyhamn, × 50. A. Female valve, No. G 315 (holotype). B. Tecnomorph, No. G 316. C–E. Specimens in ventral view, anterior end up. C. Tecnomorphic carapace, No. G 317. D. Fragmentary female valve, No. G 318. E. Female carapace, No. G 319.

Remarks.—The difference between *Apatobolbina* and the two *Leptobolbina* spp. is shown in Fig. 43. The American *Apatobolbina* spp. are nearer to *Leptobolbina* as to the morphology of the velar edge in the cruminal region than are the species from Gotland.

Occurrence.—Baltoscandia, known only from Gotland, occurring there in the Lower Visby and Slite Beds.

Leptobolbina hypnodes n.sp.

Figs. 43 B and 50.

Derivation of the Name.—Latinized Greek *hypnodes*, sleepy, referring to the "closed eye" appearance of the dolonoid scar.

Holotype.—A left female valve, No. G 315 (Fig. 50A).

Type Stratum and Type Locality.—Lower Visby Beds at Nyhamn, Gotland.

Diagnosis.—*Leptobolbina* with granulose surface lacking all traces of lobation, a tubulous, medium wide velum, and a toric ridge near the velar edge. Dolonoid scar occypying about a fourth of the length of the crumina.

DESCRIPTION.—Dorsum very low, muscle spot distinct. Velum broad and frill-like anteriorly in the male, tubulosity discernible in lateral view along all the velum in both sexes. Torus consisting of a low, striate ridge. Lateral surfaces almost evenly granulose, subvelar field finely granulose (Fig. 50).

DIMENSIONS.—Hinge length–adductorial height of five specimens from the type locality, in microns:

705–690, 680–630, 670–605, 665–700, 630–545.

REMARKS.—*L. hypnodes* differs from *L. quadricuspidata* by the lack of remnants of an anterior lobe, by the size, site, and shape of the dolonoid scar, by the position of the torus, and by the ornamentation. Stratigraphically they are very widely separated from each other.

OCCURRENCE.—Lower Visby Beds: Nyhamn, Nyhamn Well, Gustavsvik, Buske.

Leptobolbina quadricuspidata n.sp.

Figs. 43C, 49, and 51.

DERIVATION OF THE NAME.—Latin *quattuor*, four, and *cuspidatus*, provided with cusps, referring to the approximate number of spinules protruding over the hingeline.

HOLOTYPE.—A left female valve, No. G 325 (Fig. 51F).

TYPE STRATUM and TYPE LOCALITY.—Slite Beds at Follingbo I, Gotland.

DIAGNOSIS.—*Leptobolbina* with a spinulose surface and a small remnant of the cuspidal part of an anterior lobe. Velum narrow, flange-like. Dolonoid scar reduced to a pit occupying less than about $\frac{1}{7}$ of the length of the crumina; inserted flap sometimes hardly discernible.

DESCRIPTION.—The cuspidal remnant of an anterior lobe protrudes slightly over the hingeline and becomes obsolete half-way to the anteroventral margin. Dorsum hardly discernible. Velar flange broadest anteroventrally; a faint tubulosity can be traced. Velar edge in the female interrupted only by the small dolonoid scar. The velar edge clearly disappears into the pit in specimens from the south-western part of the distribution area; in the north-eastern part (Vallstena, etc.) the pit mostly or always merely seems to divide the edge of the velum, having been displaced to the most distal position possible.

DIMENSIONS.—Hinge length–adductorial height in five female specimens from the type locality, in microns:

720–630, 690–685, 685–645, 680–705, 670–625.

OCCURRENCE.—Slite Beds: Alby, Längars, Hide, Slite I, Gane, Vallstena, Follingbo I, Follingbo III.

Genus *Bolbibollia* ULRICH & BASSLER 1923

Fig. 52.

TYPE SPECIES.—*Bolbibollia labrosa* ULRICH & BASSLER 1923, by original designation (ULRICH & BASSLER 1923, p. 301).

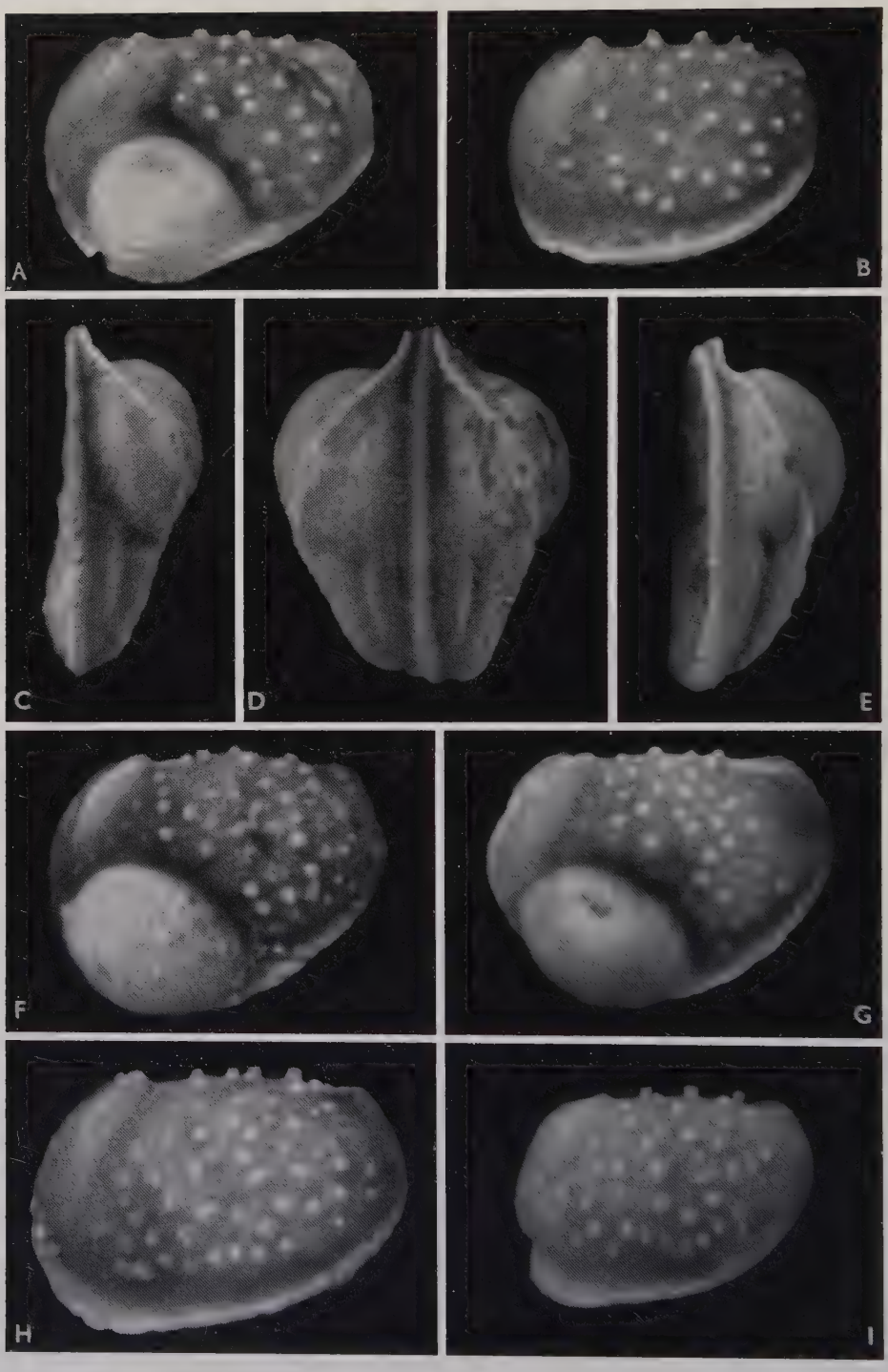


Fig. 51. *Leptobolbina quadricuspidata* n.sp. Text on opposite page.

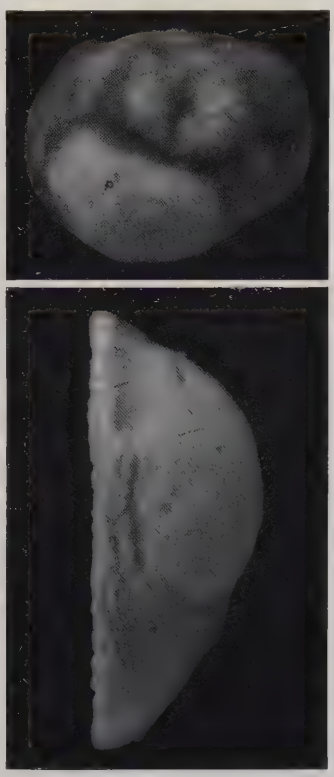


Fig. 52 A. *Bolbibollia labrosa* Ulrich & Bassler 1923, Jupiter Formation, East Jupiter Cliff, Anticosti, Quebec, Canada. Female valve, lateral view. × 50. No. NA 73.

Fig. 52 B. Same specimen, ventral view, anterior end up. × 75.

Attention is drawn to the genus *Moierina* Abušik 1960 mentioned in the Addendum, p. 359, from the Lower Ludlovian of Siberia. It lacks lobation like *Apatobolbina*, but has a crumina incorporating much of the carapace wall like *Bolbibollia*. The ventral morphology of this crumina is still unknown.

Species.—*Bolbibollia labrosa* Ulrich & Bassler 1923.

Diagnosis.—Very small *Craspedobolbininae* with the velum reduced to a ridge in the tecnomorphs; in the female the non-cruminal part of the velum is reduced to a bend. Dolonoid scar forming a simple furrow. Only lobal features a preadductorial node united over the zygal region with a swollen part of an otherwise obsolete syllobium.

Remarks.—Topotype material of the generotype has been studied (cf. Fig. 52). Ulrich & Bassler (1923, Fig. 15: 16 18) have overemphasized the velar structure and the lobation (cf. recent better figures in lateral view by Kesling & Rogers 1957, Pl. 130; Kesling's new reconstruction, 1957b, Pl. V, figs. 4–5, seems to have been somewhat influenced by that presented by Ulrich & Bassler; the dolonoid scar has been omitted.)

Fig. 51. *Leptobolbina quadricuspidata* n.sp., Slite Beds. A–D from Vallstena, E–I from Follingbo I. × 50. A–B. Female and male valves, Nos. G 320 and G 321. C–D. Female specimens in ventral view, anterior end up. C. Left valve, No. G 322. D. Carapace, No. G 323. E. Left valve, No. G 324. F. Female valve, No. G 325 (holotype). G. Female valve, No. G 326. H. Male valve, No. G 327. I. Younger tecnomorph, No. G 328.

Genus *Bolbineossia* Kesling, Heany, Kauffman, & Oden 1958

Type Species.—*Bolbineossia dictyosa* Kesling, Heany, Kauffman, and Oden 1958, by original designation.

Diagnosis.—Reticulate *Craspedobolbininae* with lobation and sulcation reduced to a small, distinct adductorial pit, occasionally in connection with a faint sulcal depression, and a syllobial groove. Dolonoid scar long; both the anterior and the posterior parts of the velum encroach onto the lateroventral part of the crumina and are widely separated from the scar.

Remarks. –The reader is referred to figures in the original description (op. cit., Pl. 24, figs. 8–16; Figs. 5–7; the scar has been omitted in the reconstructive drawing, Fig. 7, but can be observed in Pl. 24, figs. 14 and 16). This genus is particularly interesting as it shows the same trends in the development of the crumina and in the simplification of the lobation as *Apatobolbina* but has advanced reticulation and shows the lower part of the sulcus and the syllobial groove as persistent features. There seems to be a faint elevation at the place of the preadductorial node in some of the figures.

Genus *Craspedobolbina* Kummerow 1924

Cf. Fig. 53.

Type Species.—*Craspedobolbina dietrichi* Kummerow 1924, by monotypy.

Subgenera.—*Craspedobolbina* (*Craspedobolbina*) Kummerow 1924
Craspedobolbina (*Mitrobeyrichia*) Henningsmoen 1954
Craspedobolbina (*Clavobolbina*) n.subg.
Craspedobolbina (*Odoniobolbina*) n.subg.

Diagnosis.—Granulose *Craspedobolbininae* with the preadductorial knob connected with the syllobium by a marked zygal arch; a syllobial groove occurs frequently. Anterior lobe always distinctly separated from the knob by a prenodal sulcus. Dolonoid scar admarginal; there is a ridge on the crumina parallel to and below the scar.

Remarks.—*Craspedobolbina* forms a very homogeneous group of ostracodes, but it is evident that it represents several developmental branches or sections, separated by minor discontinuities in the fossil record. They have been distinguished here as subgenera which, *inter alia*, fortunately results in a recombination conserving the name *Mitrobeyrichia* for the two most important species frequently occurring with this name in the literature of the last seven years.

Occurrence.—Silurian of Europe.

Subgenus *Craspedobolbina* (*Craspedobolbina*) Kummerow 1924

Type Species.—As for the genus.

Diagnosis.—*Craspedobolbina* species with a zygal crista reaching onto the preadductorial knob.

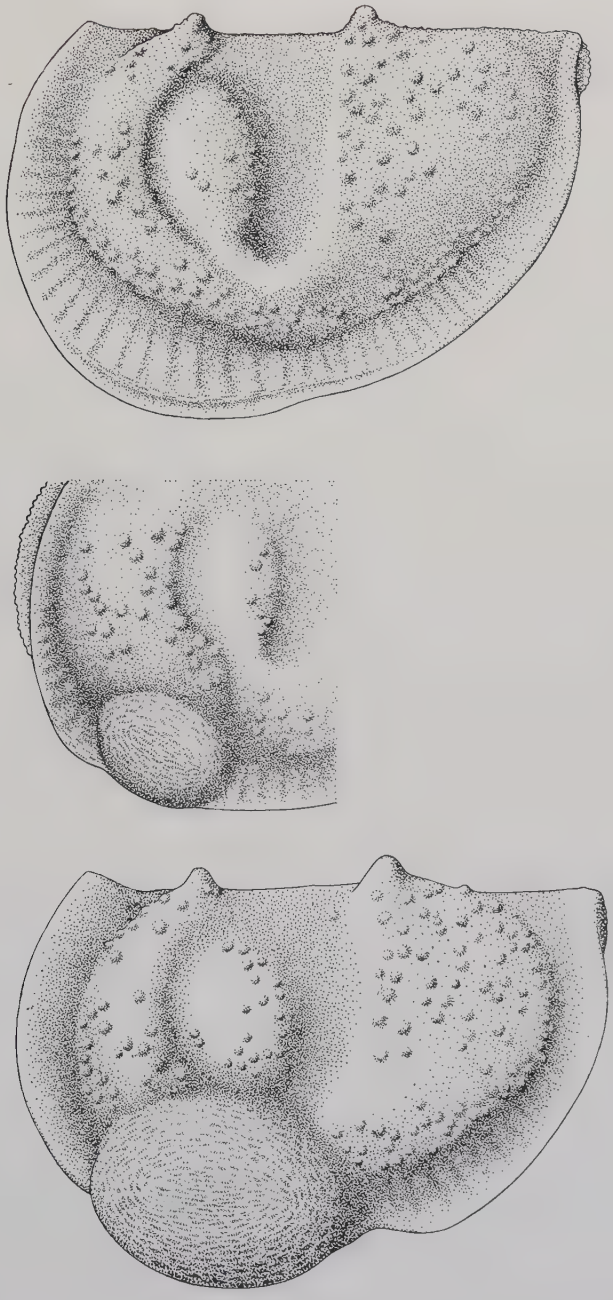


Fig. 53. *Craspedobolbina* KUMMEROW 1924, illustrated by *Craspedobolbina* (*Mitrobeyrichia*) *variolata* n.sp. (granulosity omitted). × 40. Tecnomorph (based on No. G 204), female showing incomplete cruminal metamorphosis (based on No. G 205), and normal female (based on No. G 206).

Species.—*Craspedobolbina* (*Craspedobolbina*) *perornata* n.sp.
Craspedobolbina (*Craspedobolbina*) *mucronulata* n.sp.
Craspedobolbina (*Craspedobolbina*) *juguligera* n.sp.
Craspedobolbina (*Craspedobolbina*) *ornulata* n.sp.
Craspedobolbina dietrichi Kummerow 1924

General Description of the Species.—The carapace morphology is so similar in the different species of this subgenus that all differences from the general pattern can be united in the diagnoses. In order to avoid lengthy repetitions a general description is given here:

Preadductorial knob distinct, connected with the syllobium by a cristate zygal arch and separated from the anterior lobe by a shallow (in *C. ornulata* and *C. dietrichi* very shallow) prenodal sulcus. Syllobial groove absent or hardly discernible. Velum with a thickened edge and an ornamental ridge almost confluent with the edge on the outer side of the velum in *C. perornata C. mucronulata*, and *C. juguligera*; in *C. ornulata* and *C. dietrichi* the edge is sharp. Tubuli wide, not very distinct externally, as a rule hardly discernible in *C. perornata*. The velum is inconsiderably constricted on both sides of the crumina which is of the invariable *Craspedobolbina* type (Fig. 55C). Very evenly granulose ground ornamentation. All species have an orimentary verrucosity; externally the verrucae look like enlarged, hollow granules (Fig. 13B). Crumina smooth. The varied cristae (see diagnoses) consist of the following elements: A zygal crista across the preadductorial node, interrupted on the zygal arch or immediately behind it, or extending across the syllobium in the direction of its highest point; another crista on the cusp of the anterior lobe, occasionally distinct farther down on the lobe; a third crista on the cusp or cuspidal plica of the syllobium, reaching the upper part of the syllobium. Acroidal processes even in adult specimens.

Craspedobolbina (*Craspedobolbina*) *perornata* n. sp.

Figs. 54E–H.

Derivation of the Name.—Latin *perornatus*, abundantly ornamented, referring to the well developed cristae.

Holotype.—A left female valve, No. G 329 (Fig. 54E).

Type Stratum and Type Locality.—Slite Beds at Båta, Fårö.

Diagnosis.—*Craspedobolbina* (*Craspedobolbina*) sp. with cristae on the anterior lobe and on the syllobial cusp. Zygal plica reaching across the syllobium, ending below the syllobial cusp. Tubuli not visible in incident light.

Dimensions.—Hinge length–sulcal height of female valves: Båta 1425 μ – 840 μ, 1285 μ – 810 μ. Stora Banne 1350 μ – 930 μ.

Remarks.—The inflation of the crumina results in the obsoletion of the crista anteroventrally on the ventral lobe. This species differs from all other craspedobolbinines by its long zygal crista.

Occurrence.—Lower parts of the Slite Beds: Båta, Stora Banne.

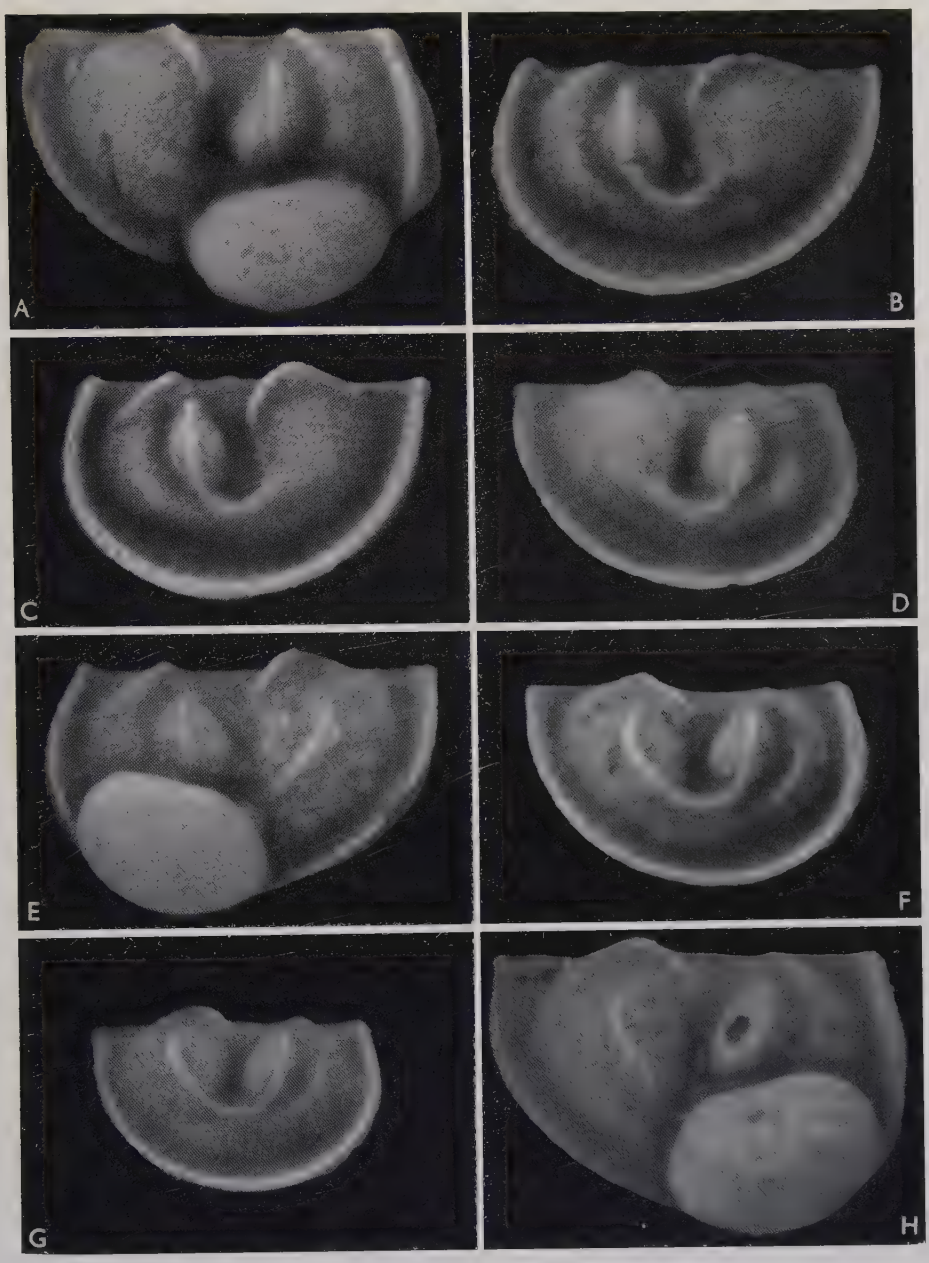


Fig. 54. A–D. *Craspedobolbina* (*Craspedobolbina*) *mucronulata* n.sp., Slite Beds, Båta. ×40. A. Female valve (holotype), No. G 333. B–D. Tecnomorphs, Nos. G 334, G 335, and G 336. E–H. *Craspedobolbina* (*Craspedobolbina*) *perornata* n.sp., Slite Beds, E–G from Båta, H from Stora Banne. ×40. E. Female valve, No. G 329 (holotype). F–G. Tecnomorphs, Nos. G 330–331. H. Female valve, No. G 332.

Craspedobolbina (*Craspedobolbina*) *mucronulata* n.sp.

Figs. 54A–D.

Derivation of the Name.—Latin *mucronulatus*, provided with a small, pointed edge, referring to the arrangement of the syllobial cristae.

Holotype.—A right female valve, No. G 333 (Fig. 54A).

Type Stratum and Type Locality.— Lower part of the Slite Beds at Båta, Fårö.

Diagnosis. —*Craspedobolbina* (*Craspedobolbina*) sp. with cristae on the cusp of the anterior lobe and on the cuspical plica of the syllobium; this crista extends down along the uppermost part of the adductorial sulcus. The zygal crista becomes gradually obsolete near the junction of the zygal arch with the syllobium. Velar tubuli very distinct in the tecnomorphs.

Remarks.—The species differs from *C. juguligera* particularly by the gradual obsoletion of the zygal crista and the shape of the cuspidal plica of the syllobium (Figs. 54 and 55). The velar edge is somewhat thinner in *C. juguligera*.

At Båta this species and *C. perornata* are represented in the same samples. It is uncertain whether the samples cut two chronodemes or whether the species lived sympatrically (size grouping of other ostracodes in the samples suggests the existence of more than one ecodeme). In any case, and though there are no intermediate forms, an intraspecific grouping of forms with a long and a short zygal crista would be genetically possible. However, there is a complete covariation in cristal and velar morphology, and each species occurs without the presence of the other in the other localities.

Occurrence. —Tofta Beds: Annelund (one, unusually large, female specimen) Lower parts of the Slite Beds: Båta, Stuks.

Craspedobolbina (*Craspedobolbina*) *juguligera* n.sp.

Fig. 55.

Derivation of the Name.—Latin *juguliger*, carrying a small yoke.

Holotype.—A left female valve, No. G338 (Fig. 55 B).

Type Stratum and Type Locality.—Upper Visby Beds at Snäckgärdsbaden, Gotland.

Diagnosis.—*Craspedobolbina* (*Craspedobolbina*) sp. with a small cristate cusp on the anterior lobe and a cristate rounded cuspidal plica on the syllobium. In the tecnomorphs the zygal crista is abruptly interrupted immediately behind the adductorial sulcus. Velum narrow, tubules distinct.

Dimensions.—Hinge length–sulcal height of five female valves from the type locality, in microns:

1105–730, 1160–760, 1120–725, 1110–690, 1105–745. See also a dispersion diagram, Fig. 23.

Remarks.—This species is distinguished from the preceding particularly

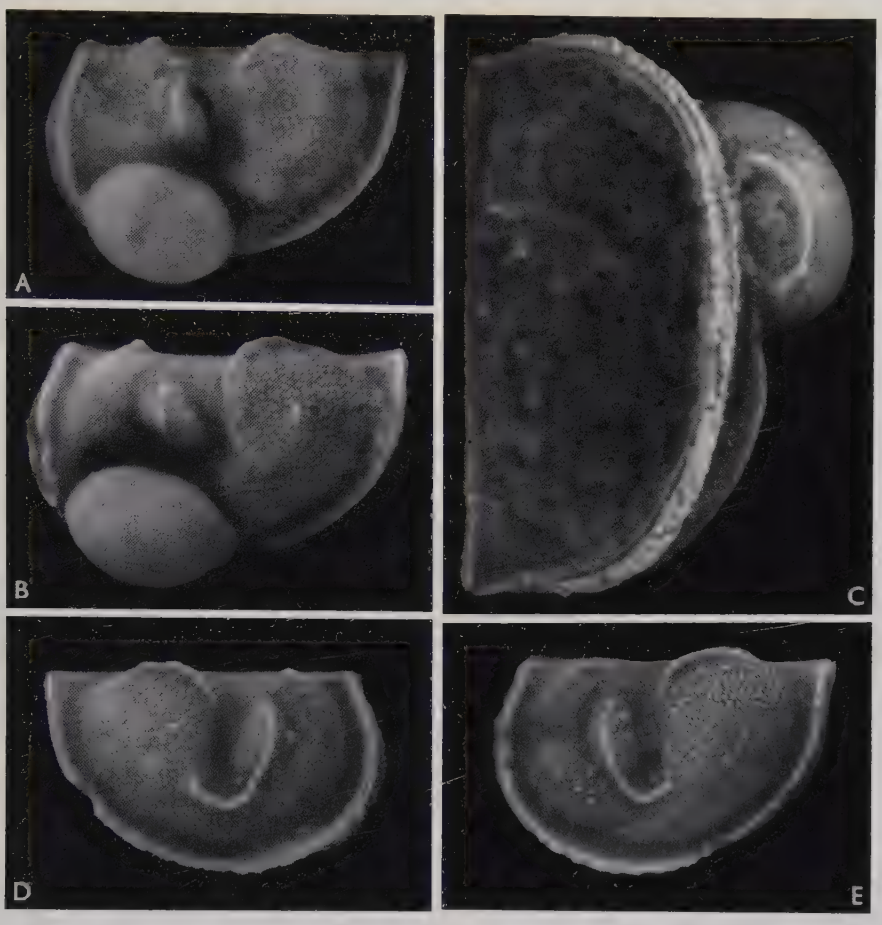


Fig. 55. *Craspedobolbina* (*Craspedobolbina*) *juguligera* n.sp. A. Female valve, Upper Visby Beds, Irevik I, No. G 337. ×40. B. Female valve, Upper Visby Beds, Snäckgärdsbaden, No. G 338 (holotype). ×40. C. Female valve, oblique ventral view, anterior end up, Upper Visby Beds, Irevik I, No. G 339. ×60. D. Tecnomorphic valve, Upper Visby Beds, Snäckgärdsbaden, No. G 340. ×40. E. Tecnomorphic valve, Upper Visby Beds, Snäckgärdsbaden, No. G 341. ×40.

by the abrupt termination of the zygal crista and the gently rounded contour of the cuspidal plica of the syllobium.

Occurrence.—Lower Visby Beds: Nyhamn (very rare). Upper Visby Beds: Halls Huk, Snäckgärdsbaden, Gnisvärd. Högklint Beds: ?Västös.

Craspedobolbina (*Craspedobolbina*) *ornulata* n.sp.

Fig. 56.

Derivation of the Name.—Latin *ornulatus* (by insertion of a diminutive of the contracted *ordin-*), "provided with only a small ornament".

Holotype.—A right female valve, No. G342 (Fig. 56A).

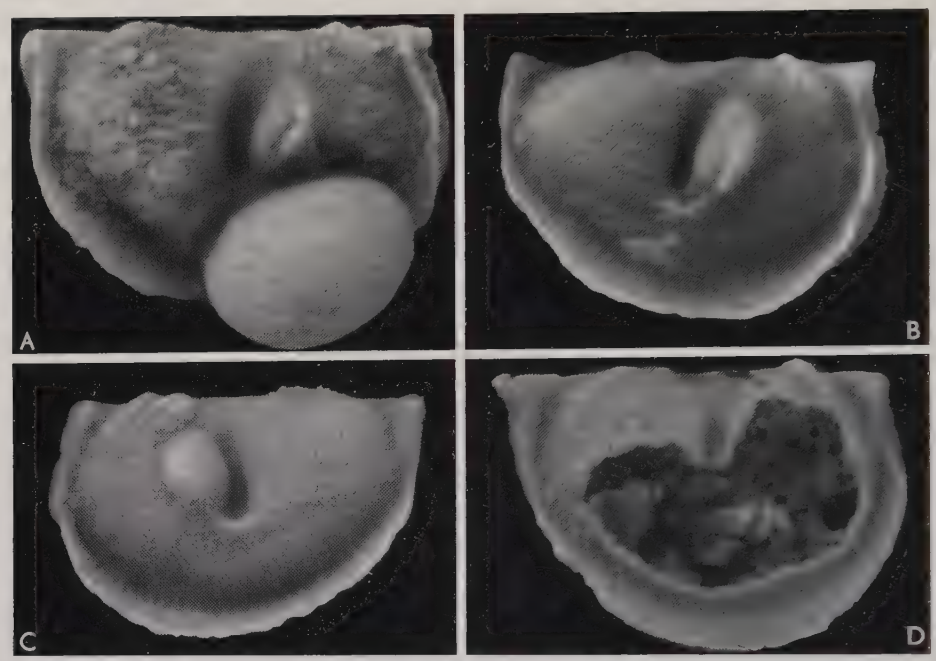


Fig. 56. *Craspedobolbina* (*Craspedobolbina*) *ornulata* n.sp. Upper Visby Beds. ×40. A. Female valve, Lickershamn II, No. G 342 (holotype). B. Tecnomorph, Visby II, No. G 343. C. Tecnomorph, Lickershamn II, No. G 344. D. Tecnomorph, fragmentary large tecnomorph (adult male) with acroidal process, Visby II, No. G 345.

Type Stratum and Type Locality. — Middle parts of the Högklint Beds, at Lickershamn II.

Diagnosis.—*Craspedobolbina* (*Craspedobolbina*) sp. without crista on the syllobial dorsal plica. Anterior lobe with sharp cusp. Zygal crista forming a club-like swelling on the preadductorial knob, obsolete before reaching the syllobium. Velum sharp-edged.

Dimensions.—Hinge length–adductorial height of two female specimens from the type locality: 1415 μ – 900 μ, 1410 μ – 930 μ.

Remarks.—The acroidal processes persist even in adult specimens (Fig. 64).

This is the species most similar to the type species, *Craspedobolbina dietrichi*, from which it differs by the absence of a cuspidal crista on the syllobium and the relative height of the valve below the zygal arch. The club-like swelling of *C. dietrichi* is less distinct; its verrucosity is more distinct, and the zygal crista does not completely efface the granulation on the zygal arch.

Occurrence.—Middle part of the Högklint Beds: Irevik II, Lickershamn II, Visby II.

Craspedobolbina (*Craspedobolbina*) *dietrichi* Kummerow 1924

Fig. 13.

1924 *Craspedobolbina Dietrichi* n.gen. n.sp.—Kummerow, p. 427; Pl. 20, Figs. 27–28.
1941 *Craspedobolbina* Kummerow 1924 ("einzige Art")—Schmidt, pp. 6, 27, and 30.

1954 *Craspedobolbina dietrichi* KUMMEROW 1924—HENNINGSMOEN, p. 46; Fig. 5 (below).
1955 *Craspedobolbina dietrichi* KUMMEROW, 1924—HENNINGSMOEN, p. 241; Fig. 3.
1957 *Craspedobolbina dietrichi* KUMMEROW—KESLING 1957 b, p. 63.

LECTOTYPE (designated herein, p. 33). — A right tecnomorphic valve in KUMMEROW's collections, determined by him (Fig. 13). The erratic origin of the material prevents normal designation and treatment of a type locality and a type stratum. The strongest indication as to its age is provided by the preceding species which is Early Wenlockian.

DIAGNOSIS.—*Craspedobolbina* (*Craspedobolbina*) sp. with small cristal ridges on the cuspidal parts of the syllobium and the anterior lobe. Diffuse club-shaped crista on the preadductorial node. Sharp-edged velum.

REMARKS.—Characters distinguishing this species from *C. ornulata* have been given above.

The identification of the species is based on the tecnomorphic specimen figured by KUMMEROW; the female of this tecnomorph cannot possibly be expected to have the appearance of the fragmentary female specimen figured by him. The velum is preserved both in the lectotype and in the tecnomorph figured by KUMMEROW, but in the other specimens, as well as in KUMMEROW's female specimen, it has been broken away. It was probably this fact that led HENNINGSMOEN (1954) to associate *Craspedobolbina dietrichi* with a group of European primitive zygobolbids with a more or less distinct zygal arch, similar to the craspedobolbinine type. *Craspedobolbina dietrichi* has been regarded by different authors (see synonymy list) as a key species in beyrichiid phylogeny and systematics, and this is still true for the genus *Craspedobolbina* after the present revision.

Neither the concomitant fauna nor the lithology as described by KUMMEROW (op. cit.) can be accepted as definite criteria in assigning an Ordovician age to the species.

OCCURRENCE.—Glacial erratics, probably of Wenlockian or Llandoverian age, in northern Germany.

Subgenus *Craspedobolbina* (*Mitrobeyrichia*) HENNINGSMOEN 1954

Fig. 53.

TYPE SPECIES.—*Beyrichia Jonesii* BOLL 1856, by original designation.

SPECIES.—*Craspedobolbina* (*Mitrobeyrichia*) *unculifera* n.sp.
Craspedobolbina (*Mitrobeyrichia*) *sinnarvensis* n.sp.
Beyrichia lunata KOLMODIN 1869
Beyrichia Jonesii BOLL 1856
Craspedobolbina (*Mitrobeyrichia*) *variolata* n.sp.
Craspedobolbina (*Mitrobeyrichia*) *insulicola* n.sp.
Craspedobolbina (*Mitrobeyrichia*) *percurrens* n.sp.
Craspedobolbina (*Mitrobeyrichia*) *lembodes* n.sp.

Beyrichia clavata KOLMODIN 1869
Craspedobolbina (*Mitrobeyrichia*) *robusta* n.sp.
Craspedobolbina (*Mitrobeyrichia*) *cuspidulata* n.sp.

DIAGNOSIS.—*Craspedobolbina* spp. without cristae but with a clearly distinguished anterior lobe, protruding over the hingeline with a cusp. Velum medium-wide, with edge thickened by the torus and a usually distinctly developed ornamental ridge, simply constricted on both sides of the crumina.

REMARKS.—This subgenus contains many of the most critical species from the systematic point of view. It is evident that there is a considerable variation in many species, geographically as well as stratigraphically, affecting size as well as ornamental and minor lobal features. With the scattered samples —mixing chronodemes and ecodemes—used for this study it is often theoretically impossible to distinguish between intraspecific and interspecific discontinuities in the long variational series provided by the material belonging to this subgenus. It would be interesting to analyse these problems by more refined biostatistical methods, but it is evident that this would be of much more value if based on special field work with greater sampling intensity and a sampling method that aims at avoiding the crossing of ecodeme boundaries. In spite of the large number of species described, the treatment of this material is in some instances characterized by "lumping" tendencies; this has taken place especially when the variational groups have no support in possible sympatric occurrences or in obvious geographical or stratigraphical isolation.

Craspedobolbina (*Mitrobeyrichia*) *unculifera* n.sp.

Figs. 42:4, 57, and 58.

DERIVATION OF THE NAME.—Latin *unculifer*, bearing a little hook, referring to the zygal ridge as the only more prominent feature on the lateral side of the valve.

HOLOTYPE.—A left female valve, No. G348 (Fig. 57C).

TYPE STRATUM and TYPE LOCALITY.—Lowermost part of the Högklint Beds at Visby I, Gotland.

DIAGNOSIS.—*Craspedobolbina* (*Mitrobeyrichia*) sp. with a rounded cuspidal plica on the syllobium and evenly granulose lobes without any tendency to lobular differentiation; the syllobial groove is barely discernible as a streak of finer granulation. Zygal arch openly U-shaped, causing a certain fusion of granules but not forming a crista.

DESCRIPTION.—Most of the few carapace differentiations are included in the generic and specific diagnoses. The velum is medium-wide, distinctly tubulous especially anteroventrally where the velar edge is more distinctly separated from the outer ornamental list than elsewhere along the velum. Material from the upper part of the stratigraphical range in the Tofta Beds might seem rather different as to the habitus, but it is preserved in a matrix of very different

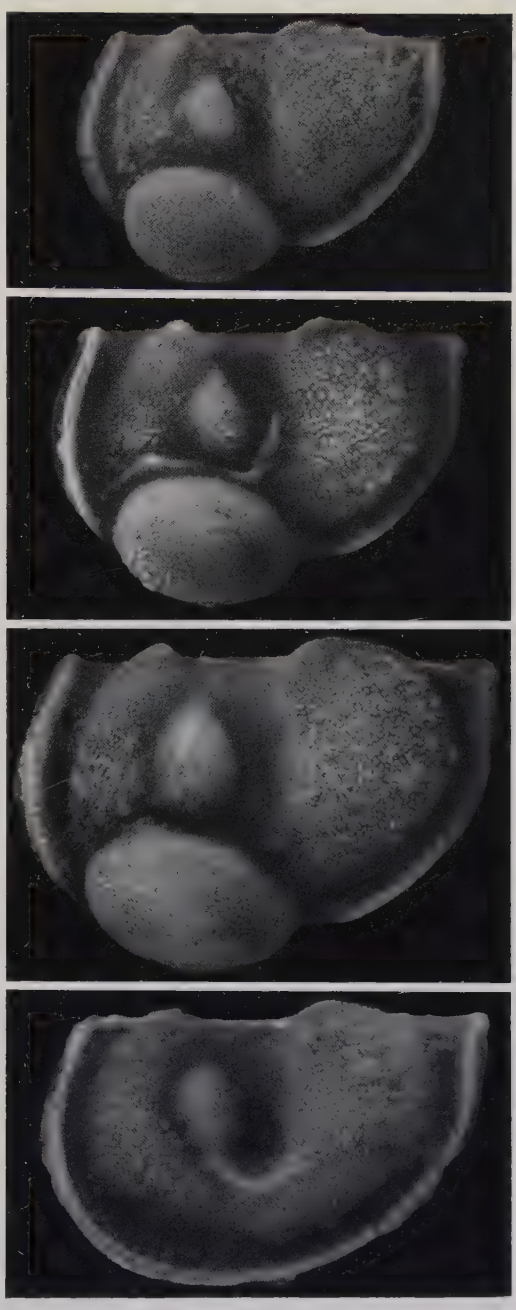


Fig. 57 A. *Craspedobolbina* (*Mitrobeyrichia*) *unculifera* n.sp., Lower Visby Beds, Gustavsvik, female valve, No. G 346. × 30.

Fig. 57 B. Same species, Högklint Beds, Visby I, female valve, No. G 347. × 30.

Fig. 57 C. Same species, Högklint Beds, Visby I, female valve, No. G 348 (holotype). × 30.

Fig. 57 D. Same species, Högklint Beds, Visby I, tecnomorphic valve, No. G 349. × 30.

composition; both in this and other species the surface ornamentation tends to become effaced in samples from the marls with "*Spongiostroma*" in the Tofta Beds (Fig. 58).

The crumina in well-preserved specimens is granulose like the lobes, but

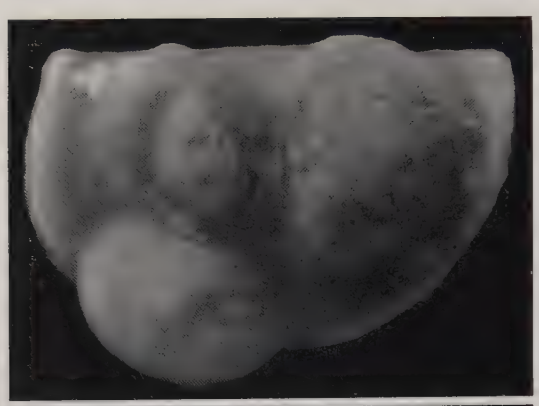


Fig. 58 A. *Craspedobolbina* (*Mitrobeyrichia*) *unculifera* n.sp. Tofta Beds, Bingers. Female valve, No. G 350. ×40.

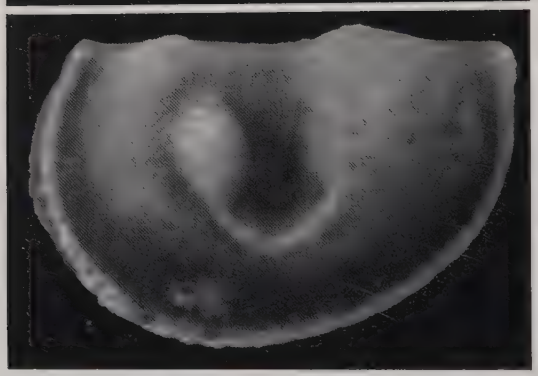


Fig. 58 B. Same species, same locality. Male valve, No. G 351. ×40.

the granules tend to arrange themselves into subhorizontal rows corresponding to the striation or rugulosity found on the crumina in other species. On the inner ventral part of the crumina the flap can often be found inserted into the dolonoid scar in a very illustrative manner; the edges of the flap have even become somewhat staved by contact with the narrower rim of the dolonoid opening (Fig. 42: 4). The acroidal processes persist even in adult specimens.

Dimensions.—There is a wide variation in size dispersion of the species in different samples; however, the variation seems to be fairly limited in samples of about the same age. Generally it can be stated that the species increases steadily in size from the Lower Visby Beds to the Högklint Beds but becomes considerably smaller again in the Tofta Beds. This is incompletely illustrated by the following measurements (hinge length–sulcal height of female valves in microns):

Lower Visby Beds, Nyhamn: 1380–880, 1350–825, 1340–870, 1320–825, 1305–850, 1300–840, 1290–865, 1240–785.

Upper Visby Beds, Snäckgärdsbaden: 1970–1200, 1935–1230, 1895–1160, 1850–1300, 1830–1185, 1795–1180, 1765–1150, 1750–1080, 1730–1160.

Högklint Beds, lowermost part, Visby I: 2070–1345, 2010–1210, 1995–1315, 1915–1245, 1885–1180, 1885–1165.

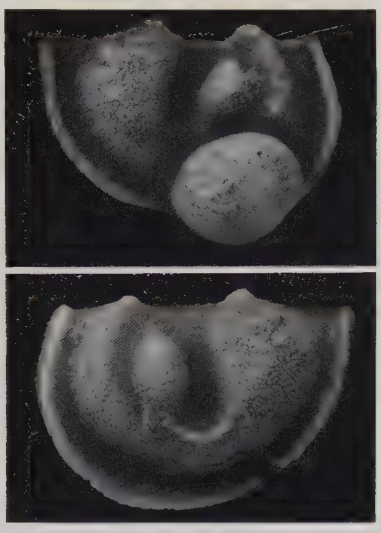


Fig. 59 A. *Craspedobolbina* (*Mitrobeyrichia*) *sinnarvensis* n.sp. Slite Beds, Sinnarve. Female valve, No. G 352 (holotype). × 30.

Fig. 59 B. Same species, same locality. Male valve, No. G 353. × 30.

Tofta Beds, Bingers: 1400–920, 1360–900, 1345–840, 1330–960. (See also size dispersion diagrams, Figs. 23 and 75.)

Remarks.—*Craspedobolbina unculifera* differs from *C. sinnarvensis* mainly by the pointed cuspidal plica and the unornamented prenodal sulcus in the latter species, which also lies below the known size range of *C. unculifera*.

Occurrence.—Lower Visby Beds: Nyhamn, Nyhamn Well, Gustavsvik, Buske. Upper Visby Beds: Irevik I, Lickershamn I, Snäckgärdsbaden, Ygne. Högklint Beds: Västös, Irevik II, Lickershamn II, Visby I. Tofta Beds: Annelund, Bingers.

Craspedobolbina (*Mitrobeyrichia*) *sinnarvensis* n.sp.

Fig. 59.

Derivation of the Name.—Latin *Sinnarvensis*, derived from the code name of the type locality (p. 49).

Holotype.—A right female valve, No. G 352 (Fig. 59 A).

Type Stratum and Type Locality.—Slite Beds at Sinnarve, Gotland.

Diagnosis.—*Craspedobolbina* (*Mitrobeyrichia*) sp. with a pointed cuspidal plica on the syllobium and evenly granulose lobes; the granulosity is effaced on the anterior lobe along the prenodal sulcus. Zygal arch openly U-shaped, causing a fusion of the granules but not forming a crista.

Description.—Velum constructed as in the preceding species; crumina granulose. See diagnosis.

Dimensions.—Hinge length–sulcal height of female valves from the type locality 1230–770, 1211–765, 1185–820.

Remarks.—This species is distinguished from *C. unculata* by its pointed

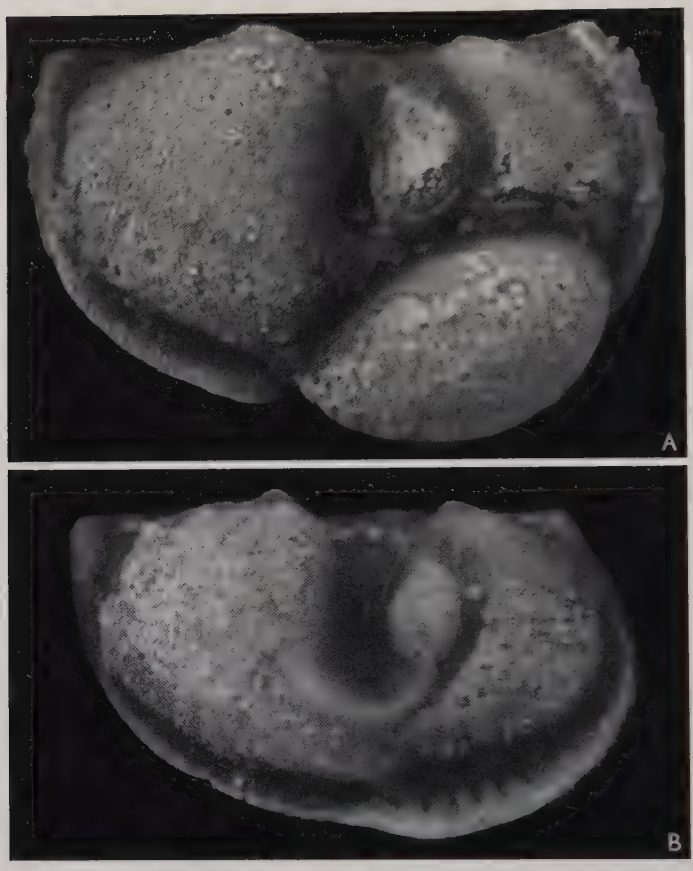


Fig. 60. *Craspedobolbina* (*Mitrobeyrichia*) cf. *lunata* (KOLMODIN 1869), Slite Beds. Svarvare. × 30. A. Female valve, No. G 354. B. Tecnomorphic valve, No. G 355.

cuspidal plica on the syllobium, the unornamented prenodal sulcus, and its small size.

OCCURRENCE.—Slite Beds: Oivide, Sinnarve, Valbytte.

Craspedobolbina (*Mitrobeyrichia*) *lunata* (KOLMODIN 1869)

Fig. 5 A, *C.*(*M.*) cf. *lunata* Fig. 60.

1869 *Beyrichia lunata* n.sp.—KOLMODIN, p. 17, Figs. 8–9.

LECTOTYPE.—A female carapace, No. G 262 (KOLMODIN 1869, Fig. 8), designated herein, p. 20 (Fig. 5 A).

TYPE STRATUM AND TYPE LOCALITY.—Silurian, Gotland (the label only states "Gotland").

DIAGNOSIS. — Large *Craspedobolbina* (*Mitrobeyrichia*) sp. with granulation evenly distributed on the lobes but effaced in both sulci. No lobular differentia-

tion in the anterior lobe. Syllobial cuspidal plica tends to be pointed near the sulcus. Velum distinctly tubulous only anteroventrally and ventrally in the tecnomorph alone, crumina inconsiderably constricted proximally.

Description.—The description refers to material represented here as *C.* (*M.*) cf. *lunata* according to Fig. 60.

Anterior lobe in the male very broad anteroventrally; preadductorial node relatively small, connected with the syllobium by a rounded, not very prominent, zygal arch. Syllobium very broad, with a cuspidal plica which tends, especially in the male, to be pointed anteriorly. Syllobial groove very shallow. Velum without externally visible tubules posteroventrally; in the tecnomorphs there are small intertubular depressions ventrally, and anteroventrally the velum tends to widen considerably and have very distinct, wide tubules. The constriction of the velum on both sides of the crumina is inconspicuous as seen in lateral view. Surface evenly granulose, except in the sulci, with evenly distributed, enlarged granules marking an orimentary verrucosity. The granulation is finer on the anterior lobe, is also found on the velum, and is very fine on the crumina where the granules are indistinctly arranged in rows.

Dimensions.—Hinge length–sulcal height. Lectotype: 2385 μ – 1710 μ. Two female valves from Svarvare: 2620 μ – 1515 μ, 2630 μ – 1785 μ.

Remarks.—The lectotype is considerably damaged by preparation—all finer details except a little of the granulation on the syllobium are effaced—and as the type locality is unknown, there is no possibility of obtaining more topotype material. Therefore, the *confer* for the new material described here has been introduced, especially as the point of the cuspidal plica cannot be verified in the lectotype.

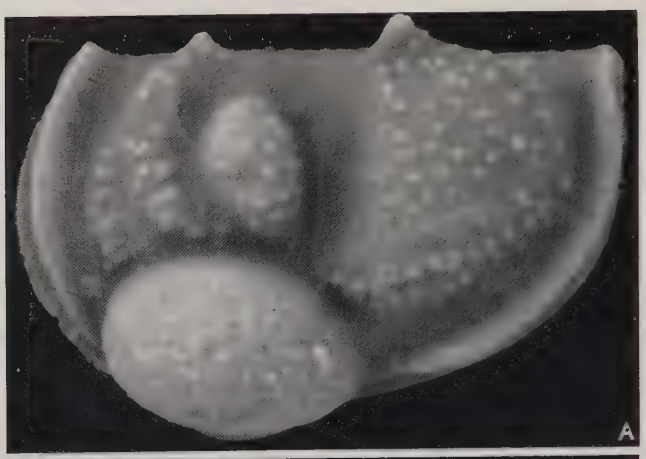
The size of this ostracode lies above the variation range of all other craspedobolbinines. The very wide connection of the crumina with the wall of the valve also distinguished it from the other species with evenly granulose, broad lobes described above.

Occurrence.—Uppermost part of the Slite Beds in the southwesternmost area of their outcrop: Svarvare. Very rare; only 9 specimens, three of them females, have been found by selective extraction of very large samples. It is very probable that the lectotype comes from one of the localities in the area between this locality and Klintehamn which are known to have been visited by several of the earliest ostracode collectors.

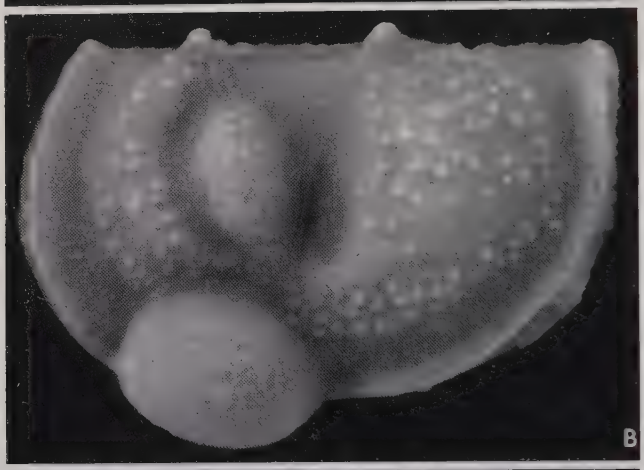
Craspedobolbina (*Mitrobeyrichia*) *jonesi* (Boll 1856)

Fig. 3A–B.

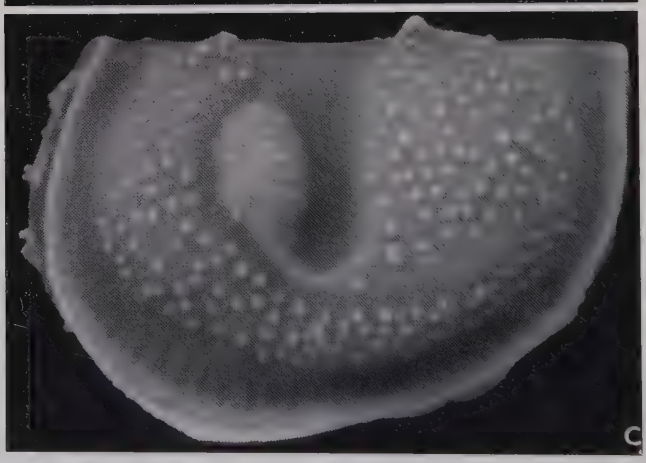
1856 *Beyrichia Jonesii* nov. sp.—Boll, p. 322; Figs. 1–2.
1888 *Beyrichia Jonesii* Boll—Kiesow, p. 13; Pl. II, figs. 10–12.
1954 *Beyrichia jonesii* Boll 1856—Henningsmoen, p. 27 (designated as type species



Female valve, No. G 356 (holotype).



Female valve with well developed but very small crumina, No. G 257.



Male valve, No. G 358.

Fig. 61. *Craspedobolbina* (*Mitrobeyrichia*) *variolata* n.sp., Slite Beds, Svarvare. × 40.

of *Mitrobeyrichia* subg. n., translated into a genus by Kesling & Rogers 1957, p. 998).

1956 *Beyrichia jonesi*—Martinsson, p. 19.

Lectotype.—A right, probably young, tecnomorphic valve figured by Boll (1856, Fig. 1), designated herein (p. 18, Fig. 3 B).

Type Stratum and Type Locality.—Cannot be designated owing to the erratic origin of the material. Boll (l.c.) regarded one of the specimens as Ordovician, the other as Silurian.

Remarks.—It is impossible to establish whether the other tecnomorphic specimen (Fig. 3 B) figured by Boll (op. cit., Fig. 2) is conspecific with the holotype. This differs from the following verrucose *Craspedobolbina variolata* by its rounded cuspidal plica on the syllobium. A survey of verrucose specimens in the erratic *Graptolithengestein* of North Germany (cf. also Kummerow 1943, Pl. II, fig. 9) shows that there exist verrucose *Craspedobolbina* species which retain the rounded cuspidal plica right through the ontogeny and which could possibly prove to include *C. jonesi*.

The name *Beyrichia jonesi* is used in older literature for most varying *Craspedobolbina* (*Mitrobeyrichia*) species, especially *C. clavata* (cf. p. 169).

Craspedobolbina (*Mitrobeyrichia*) *variolata* n.sp.

Figs. 26: 4–6, 27: 1–3, 37, 42: 2–3, 53, 61, and 62.

1960 *Beyrichia* (*Mitrobeyrichia*) sp. B—Martinsson 1960b, Figs. 1 and 2; Pl. II, figs. 4–6; Pl. III, figs. 1–3; Pl. IV, figs. 2–3.

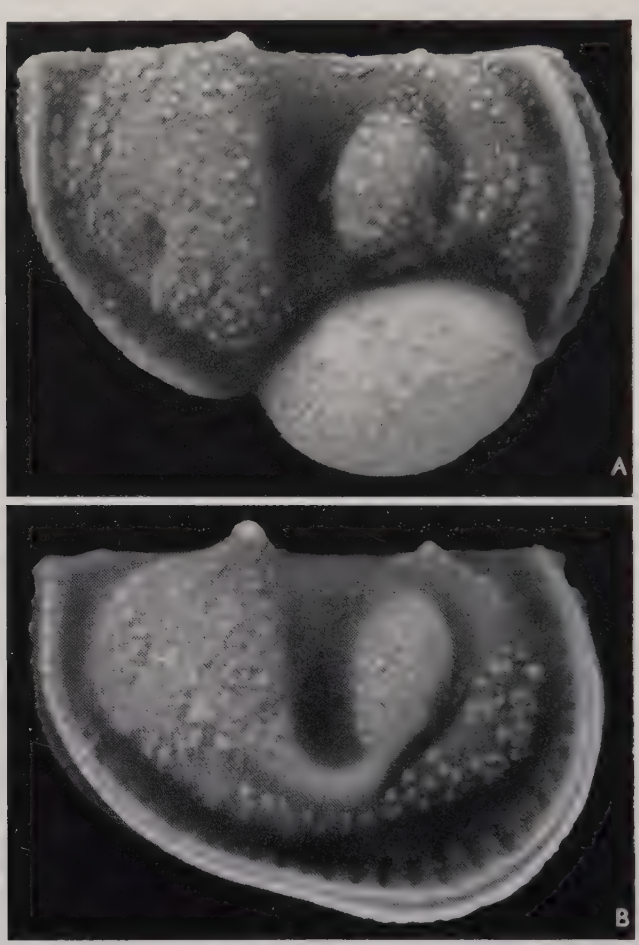
Derivation of the Name.—Latin *variolatus*, suffering from smallpox, referring to the pronounced verrucosity in this species.

Holotype.—A left female valve, No. G 356 (Fig. 61 A).

Type Stratum and Type Locality.—Uppermost Slite Beds at Svarvare, Gotland.

Diagnosis.—Verrucose *Craspedobolbina* (*Mitrobeyrichia*) sp. with sharp cuspidal points of subequal size on both anterior lobe and syllobium. A beginning of a lobular differentiation of the anterior lobe is seen in the ornamentation, and there is a streak in the ornamentation marking the site of the syllobial groove.

Description.—The prepletion and the coarseness of the granulose ground pattern vary widely, to some extent even in the same locality. The cusp of the anterior lobe is generally not much smaller than that of the syllobium but may be suppressed in some specimens. The differentiation of a field in the verrucose pattern marking the separation of an anteroventral lobule is not distinct in all specimens (cf. Fig. 61 C). The zygal arch may be thick or thin (Figs. 61 C and 62 B). The velar edge is generally thin and extended anteroventrally in the tecnomorphs and especially in the adult males; the tubules are distinct along the



Female valve, No. G 359.

Male valve, No. G 360.

Fig. 62. *Craspedobolbina* (*Mitrobeyrichia*) *variolata* n.sp., Mulde Beds. Djupvik. ×40.

larger part of the male velum; in the female they are occasionally not very distinct.

Dimensions.—Hinge length–sulcal height in ten female valves from the type locality:

1895–1200, 1890–1105, 1830–1200, 1825–1210, 1785–1125, 1775–1210, 1770–1285, 1765–1145, 1755–1110, 1665–1205 (see also Fig. 75).

Remarks.—Figs. 61 and 62 show specimens from two different localities. As seen in Fig. 26: 4 there are specimens with a more pronounced granulosity and prepletion also in the same sample as the specimens in Fig. 61. The difference in variation between the two localities, if any, is by no means as marked as might be concluded from these illustrations.

Occurrence.—Uppermost part of the Slite Beds: Svarvare. Mulde Beds: Djupvik? Considerable efforts have been made in order to complete the scarce

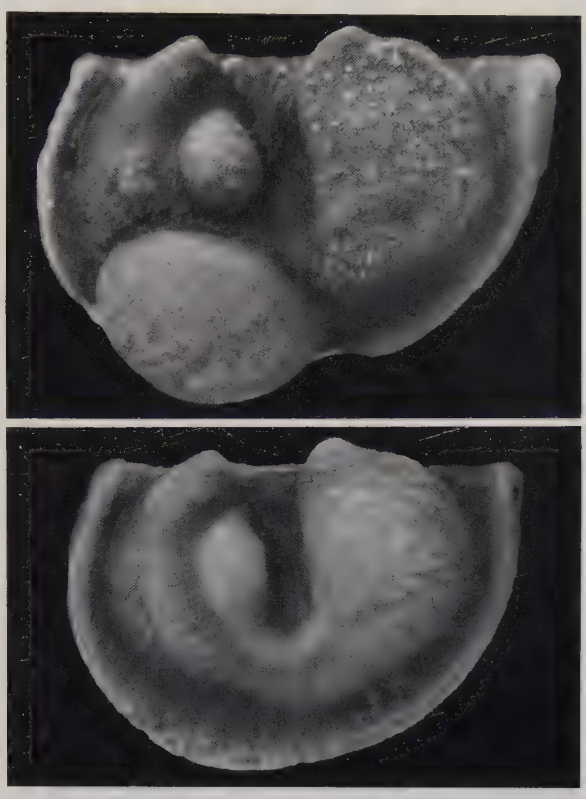


Fig. 63 A. *Craspedobolbina* (*Mitrobeyrichia*) *insulicola* n.sp. Slite Beds, Lerberget. Female valve, No. G 361 (holotype). × 30.

Fig. 63 B. Same species, same locality. Tecnomorphic valve, No. G 362. × 30.

material in a sample from the lowermost part of the sequence in the brook at Djupvik, but in vain. This is probably the only case where a contamination by decomposed erratics can be taken into consideration.

Craspedobolbina (*Mitrobeyrichia*) *insulicola* n.sp.

Fig. 63.

Derivation of the Name.—Latin *insulicola*, inhabitant of an island, referring to the occurrence of the species on Stora Karlsö.

Holotype.—A left female valve, No. G361 (Fig. 63A).

Type Stratum and Type Locality.—Slite Beds at Lerberget, Stora Karlsö.

Diagnosis.—Slightly verrucose *Craspedobolbina* (*Mitrobeyrichia*) sp. with a stout cusp anteriorly on an undulate cuspidal plica and a faint anteroventral depression. Short and deep carapace.

Description.—Very faint sulcules separate a faint anteroventral lobule and the cuspidal part from the main part of the anterior lobe. The zygal ridge is never sharply set off from the valve wall below it, and there is only occasionally a marked sulcus. Velar tubules always visible in the male, very seldom in the female velum. Crumina granulose, with some tendency towards a linear arrangement of the granules.

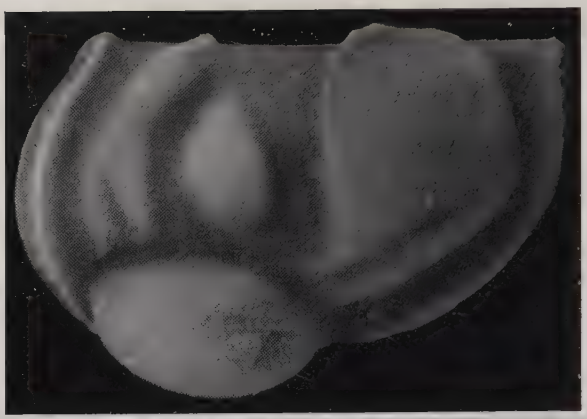


Fig. 64 A. *Craspedobolbina* (*Mitrobeyrichia*) *percurrens* n.sp., Slite Beds, Follingbo II. Female valve, No. G 363. × 30.

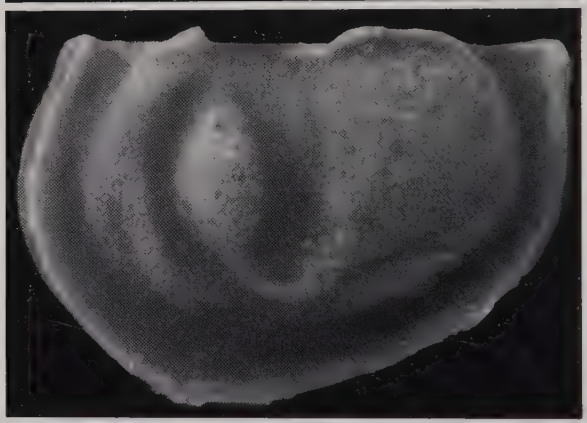


Fig. 64 B. Same species, same locality. Male valve, No. G 364. × 30.

Dimensions.—Hinge length–sulcal height in five female valves from the type locality, in microns:

2135–1460, 2095–1485, 2090–1410, 1995–1365, 1985–1350.

Remarks.—This species differs from the following by its deep flattened ventral outline, its verrucosity, and its stout cusp on the syllobial plica.

Occurrence.—Slite Beds: Valbytte, Lerberget, Västarberget.

Craspedobolbina (*Mitrobeyrichia*) *percurrens* n.sp.

Figs. 64, 65, and 66.

Derivation of the Name.—Latin *percurrens*, running through, referring to the wide stratigraphical range of the species.

Holotype.—A right female valve, No. G365 (Fig. 65A).

Type Locality and Type Stratum.—Slite Beds at Båta, Fårö.

Diagnosis.—*Craspedobolbina* (*Mitrobeyrichia*) sp. in which the zygal arch —which is rounded and gently merging with the preadductorial knob and the syllobium—curves down distinctly through the projection forwards of a line

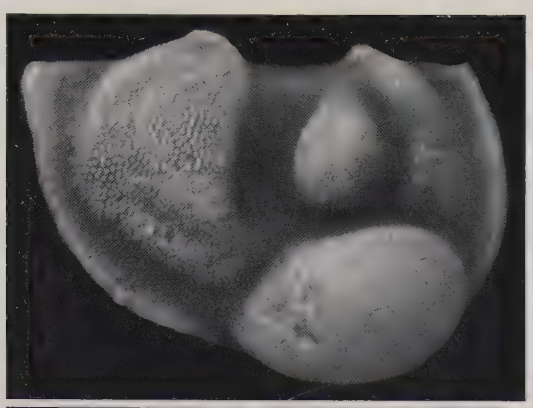


Fig. 65 A. *Craspedobolbina* (*Mitrobeyrichia*) *percurrens* n.sp., Slite Beds, Båta. Female valve, No. G 365 (holotype). × 30.

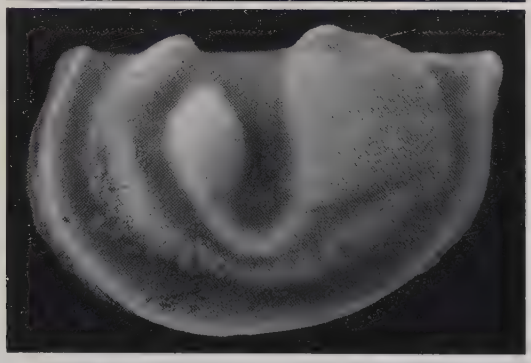


Fig. 65 B. Same species, same locality. Male valve, No. G 366. × 30.

along the well marked syllobial groove. Slight lobular differentiation in the anterior lobe. The dorsal part of the cuspidal plica of the syllobium conceals a considerable part of the hingeline in lateral view, being rounded, slightly drawn up into a rounded cusp anteriorly, or even depressed and slightly biundulate. The even granulation is never broken by a distinct verrucosity.

Description.—As may be concluded both from the length and the formulation of the diagnosis, this taxion contains a series of individuals and populations with quite considerable variations even in details specifically stable in other species.

The anterior lobe is invariably faintly subdivided into lobuli as in the preceding species. There are faint sulcular depressions separating an anteroventral lobule and the cuspidal part of the lobe from its main body. The preadductorial knob is separated from the anterior lobe by a distinct prenodal sulcus. The transition of the zygal arch towards the preadductorial knob and the syllobium is very gentle, and the arch is rounded as seen in transversal section. There is a tendency to an anteroventral depression below the preadductorial knob. The cuspidal plica of the syllobium is more varied. The most common type is a rounded cuspidal plica as shown in Fig. 66 (most of the material from the Slite–Yxne–Follingbo–Gardrungs regions), which might be markedly drawn up anteriorly into a rounded cusp (at localities on Fårö, cf.

Fig. 65, and in the Mulde and Hemse Beds)—but never having the disharmonic, staved appearance in *C. insulicola* or depressed as a biundulate ridge as in Fig. 64. This latter arrangement, found very typically only at Follingbo II but with transitional features at Stave, Vallstena, Gane, etc. is in the typical case combined with a flattening of the ventral outline which is elsewhere deeply and gently rounded.

The velum is generally markedly flange-like, even in the large tecnomorphs, so that no tubulosity or ornamental ridge or crest can be seen in incident light (Fig. 65), but material from, e.g., Follingbo I, the Slite region, and the sequence above the Slite Beds may exhibit one or both of these characteristics. The ornamentation consists of an even granulosity, obsolete in the sulci, as is almost always the case in the beyrichiids, sparse along the base of the velum but reaching onto it and also covering the crumina. A tendency to verrucosity may be traced, but it never breaks the granulose pattern.

Remarks.—There can be no great difficulty in separating several very stable variational groups from the bulk of the forms included. In that case, however, only a group of taxia largely representing one locality, or one ecodeme within it, would be obtained. On the other hand, the omission of seemingly insignificant details in the diagnosis would lead to the inclusion in the same species of *C. insulicola* and perhaps one or more of the following species. In such cases the practical determinability, without a special analysis of thousands of cleaned specimens, has had a certain bearing on the decision to separate them from *C. percurrens*.

As now defined, this species differs from *C. insulicola* mainly in the absence of verrucosity and in the shape of the cuspidal part of the syllobium; it differs from *C. lembodes* by the shape and position of the zygal arch and the shape of the cuspidal part of the syllobium. The material from Follingbo II reaches the size range of *C. lembodes* and has, like this species, a flattened ventral outline, but it never has the distinctly tubulous velum of *C. lembodes*.

The few figures selected for publication may give an impression of variational discontinuities qualitatively equal to those between other species. Such a supposition is, however, readily abandoned after the study of material from numerous samples.

Dimensions.—One of the most varying properties in this species is the size. Some minor series of measurements are given here (hinge length–sulcal height of female valves in microns). Material from different parts of the Slite Beds has been used.

Follingbo II (cf. Fig. 64): 2095–1320, 2035–1350, 2030–1250, 2250–1380, 1950–1320.

Follingbo I (cf. Fig. 66): 1765–1110, 1710–1065, 1675–1065, 1625–1085, 1485–980.

Follingbo III (with a beyrichiid concomitant fauna very different from the two preceding localities): 1750–1130, 1665–1100, 1610–1085, 1610–1080, 1550–1085.

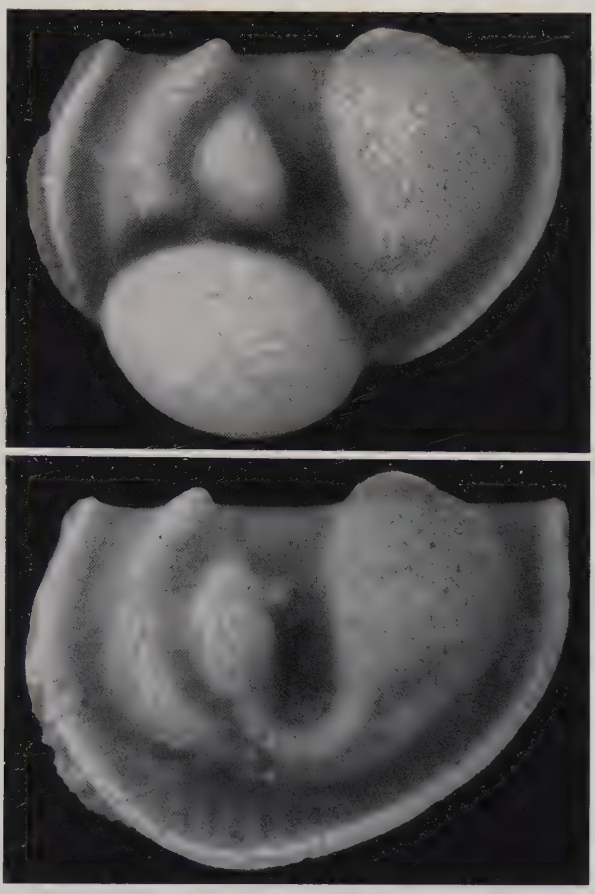


Fig. 66 A. *Craspedobolbina* (*Mitrobeyrichia*) *percurrens* n.sp., Slite Beds, Follingbo I. Female valve, No. G 367. × 40.

Fig. 66 B. Same species, same locality. Male valve, No. G 368. × 40.

Gane (mixed ecodemes?): 1955–1240, 1895–1280, 1885–1230, 1850–1150, 1815–1230, 1810–1200, 1750–1105, 1705–1020, 1665–1040, 1645–1120.

Längars: 1845–1090, 1815–1080, 1770–1130, 1730–1100, 1705–1080.

Båta: 2295–1345, 2215–1535, 2195–1345, 2030–1330, 2010–1290.

Occurrence.—Slite Beds: Båta, Haganäs, Fårö Skola, Broa, Alby, Puttarsjaus, Längars, Hide, Spillings, Slite I, Slite II, Enholmen, Yxne, Gane, Vallstena, Norrbys, Follingbo I, Follingbo II, Follingbo III, Stave, Nygårds, Gardrungs, Oivide. Halla Beds: Hörsne, Gandarve. Mulde Beds: Däpps, Djupvik? Hemse Beds: Eske, Snoder, Lukse, Petes, Hemmungs.

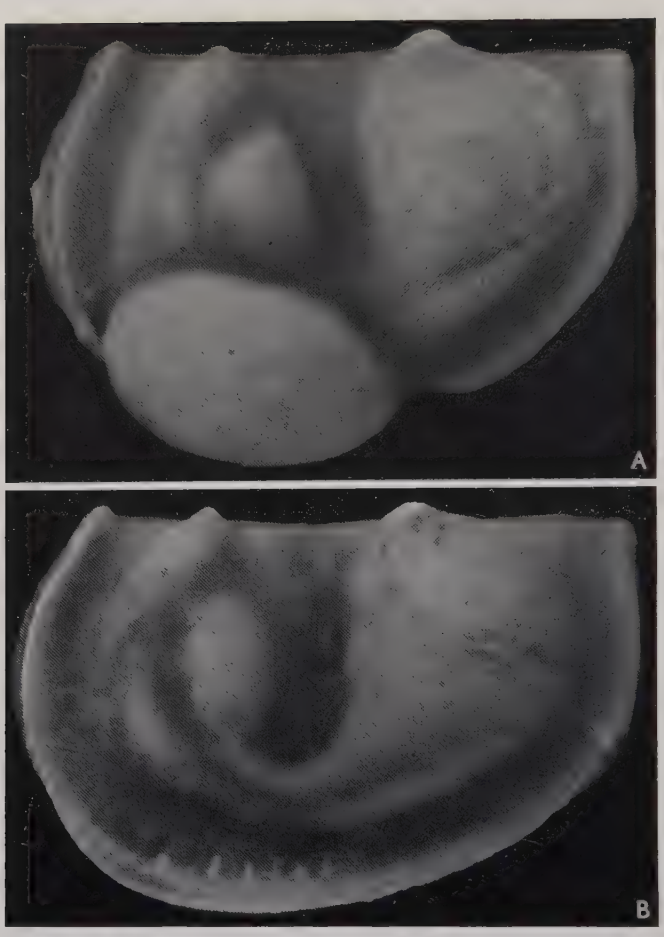
Craspedobolbina (*Mitrobeyrichia*) *lembodes* n.sp.

Figs. 67 and 68.

Derivation of the Name.—Latinized Greek *lembodes*, barge-like.

Holotype.—A left female valve, No. G 369 (Fig. 67 A).

Type Stratum and Type Locality.—Mulde Beds at Däpps, Gotland.



Female valve, No. G 369 (holotype).

Male valve, No. G 370.

Fig. 67. *Craspedobolbina* (*Mitrobeyrichia*) *lembodes* n.sp., Mulde Beds, Däpps. × 30.

Diagnosis.—*Craspedobolbina* (*Mitrobeyrichia*) sp. with the cuspidal plica of the broad syllobium drawn up into a relatively small cusp anteriorly, concealing only a relatively small part of the hingeline in lateral view. The zygal arch does not curve down considerably below a line drawn through the syllobial groove. Ventral contour of the velar edge flattened or very slightly curved.

Description.—Lobular differentiation of the anterior lobe and anteroventral depression as in the preceding species. The syllobium is broad, with a distinct groove; there is a tendency to callus formation, but this never leads to differentiation in the granulation. Velum with distinct tubulosity anteriorly in the tecnomorph; otherwise no considerable tubular depressions are to be seen. There is no anteroventral extension of the velum affecting the anteroventral contour of its edge. The granulation is even, but a faint verrucosity may be

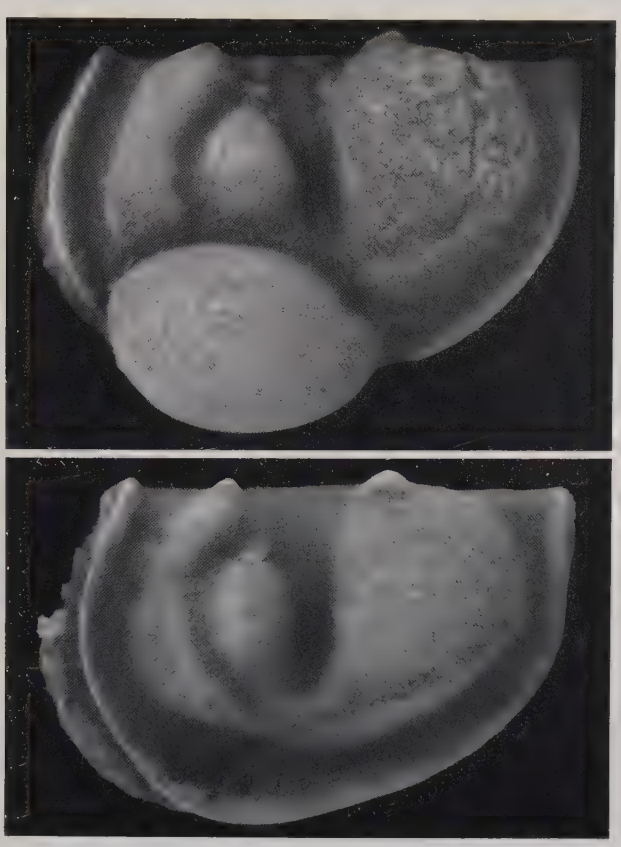


Fig. 68 A. *Craspedobolbina* (*Mitrobeyrichia*) *lembodes* n.sp., Slite Beds, Svarvare. Female valve, No. G 371. ×30.

Fig. 68 B. Same species, same locality. Male valve, No. G 372. ×30.

observed on the dorsal part of the syllobium and in the anteroventral region of the carapace. Crumina typically granulo-striate.

Dimensions.—Hinge length–sulcal height of female valves, in microns:

Slite Beds, Svarvare: 2315–1385, 2085–1410, 1995–1305, 1975–1305, 1965–1385.

Mulde Beds, Däpps: 2510–1795, 2475–1775, 2465–1715, 2280–1550, 2245–1610.

Remarks.—*Craspedobolbina lembodes* differs from *C. robusta* mainly by the morphology of the tecnomorphic velum and from *C. clavata* mainly by the relative size of the syllobium, the shape of the syllobial cusp, and the shape and ornamentation of the callus.

Occurrence. Slite Beds: Svarvare. Mulde Beds: Däpps. Klinteberg Beds: Hunninge? (distinction from *C. robusta* problematic).

Craspedobolbina (*Mitrobeyrichia*) *clavata* (Kolmodin 1869)

Figs. 5B, 16, 17A, 18, 19, 21, 24, 25, 26: 1–3, 28–33, 36: 10–11. 40F–G, and 69.

1869 *Beyrichia clavata* n.sp.—Kolmodin, p. 18; Fig. 10.
1888 *Beyrichia Jonesii* var. *clavata* Kolmodin—Kiesow, p. 15; Pl. II, Fig. 13.

1951 *Beyrichia jonesi* Boll—Spjeldnaes, pp. 745–755; Pl.s 103–104.
1954 *B. clavata* Kolmodin 1869 (subj. syn. of *jonesii* ...)—Henningsmoen, p. 27 (referred to *Mitrobeyrichia* n.subg.).
1956 *Beyrichia* (*Mitrobeyrichia*) *clavata* (Kolmodin 1869)—Martinsson, pp. 18–22; Fig. 6; Pl. I, fig. 1.
1959 *Mitrobeyrichia clavata* (Kolmodin 1869)—Pokorný, p. 322; Figs. 1–2; Pl. I (cf. Pokorný 1958, Fig. 626).
1960 *Beyrichia* (*Mitrobeyrichia*) *clavata* (Kolmodin)—Martinsson 1960b, Pl. I; Pl.II, Figs. 1–3; Pl. V, Figs. 10 and 11.
For further synonymy, cf. Martinsson 1956, p. 18.

Lectotype.—A tecnomorphic carapace, No. G145 (cf. p. 20 and Fig. 5B), designated by Martinsson 1956, p. 19.

Type Stratum and Type Locality.—Mulde Beds at Djupvik, Gotland.

Diagnosis.—*Craspedobolbina* (*Mitrobeyrichia*) sp. with medium-broad syllobium bearing one large, somewhat flattened cusp which is distinctly bent outwards. Marked, long callus below a not very distinct syllobial groove.

Description.—The lobular differentiation of the anterior lobe is as described under *C. insulicola* and *C. percurrens*. The zygal arch is rounded but very prominent; it curves markedly down from its junction with the syllobium and reaches a line drawn along the upper limitation of the callus. Syllobium as described in the diagnosis. Anteroventral depression distinct. Velum broad, always distinctly tubulous from a point near the mid-length of the anteroventral lobule to the posterior end of the callus. The granulose ground pattern is less even and distinct than in other species; it does not reach onto the velum or the crumina which is almost smooth laterally in the normal female; ventrally it has a striate or granulostriate pattern like that along the torus. There is a distinct verrucosity especially in the region of the anteroventral lobule and on the syllobium (it is possible to illustrate the pore pattern reflected in the verrucosity by photographing perfectly cleaned, in most cases preferably unfluoridized, male valves in transmitted light; an investigation of this kind could not, however, be made throughout the genus within the time schedule of this study).

The ventral morphology in this subgenus need not be dealt with in much more detail than has already been done in the generic diagnosis and in the section on ontogeny in the General Part. *C. clavata* as illustrated in Figs. 18, 19, and 25 represents the normal conditions in the subgenus. The velum has an ornamental ridge near to and outside the edge; inside it there is a corresponding thickening constituted by the distally situated, striate torus. Each valve has a vertical marginal frill divided into one anteroventral and one posteroventral crescent-shaped portion; ventrally the marginal structure is very finely tubulous, without any thickening along the edge.

Dimensions.—Hinge length of the adult female, as measured on left valves, 1840 μ – 2060 μ; height over the adductorial sulcus (="sulcal height") 1120 μ – 1360 μ. Detailed size and growth data for all moult stages and both

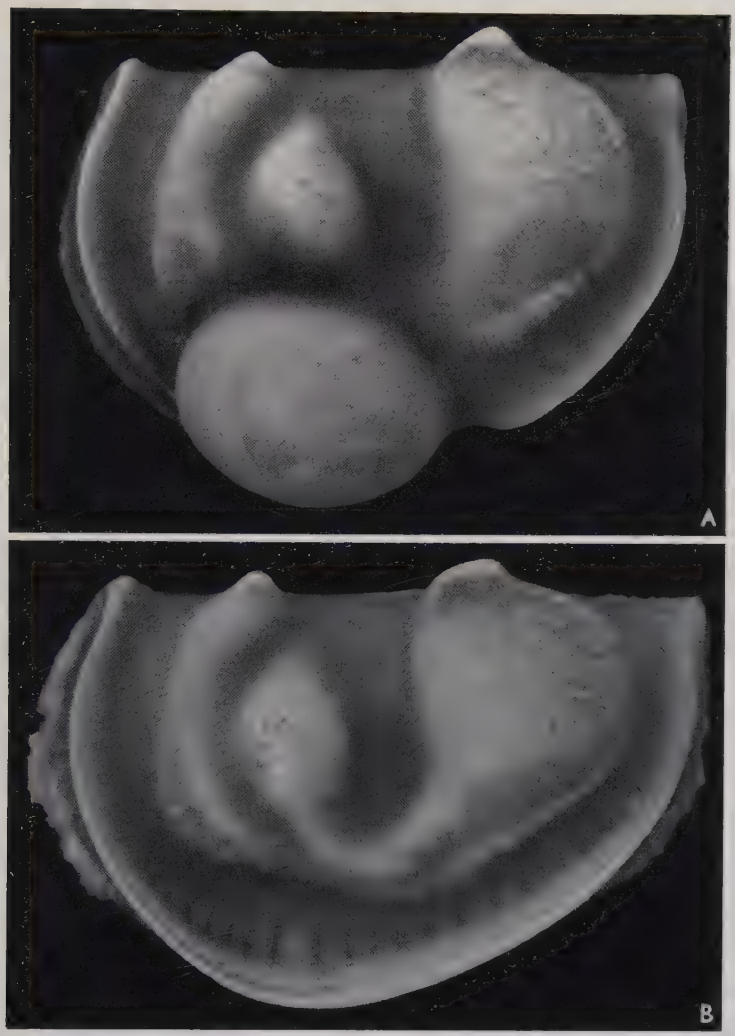


Fig. 69. *Craspedobolbina* (*Mitrobeyrichia*) *clavata* (KOLMODIN), Mulde Beds, Mulde. A. Female valve, No. G 373. B. Male valve, No. G 374. Note the wider tubule anteroventrally in the male velum. ×40.

sexes have been given by MARTINSSON 1956 (Tables 1 and 2, p. 19, and Fig. 6); cf. also Fig. 22 and 21 in this paper.

REMARKS.—The ontogeny and cruminal metamorphosis of this species have been extensively dealt with in this paper (pp. 79 sqq. and 90 sqq., etc.). Some further investigations as to the duration of the brood care, the size and number of the larval specimens in the cruminae and details of the carapace morphology are being carried out but have no immediate bearing on the main theme of this paper.

The shape of the syllobial cusp, the arrangement of the callus and the zygal

Fig. 70. *Craspedobolbina* (*Mitrobeyrichia*) *robusta* n.sp., Hemse Beds, Snoder. A Female valve, No. G 375 (holotype). B. Male valve, No. G 376. ×40.

arch, and the pronounced tubulosity of the velum, even in the female, are good differential diagnostics in comparison with the preceding species and with *C. robusta*.

Occurrence.—Mulde Beds: Klintebys, Däpps??, Mulde, Blåhäll, Djupvik.

Craspedobolbina (*Mitrobeyrichia*) *robusta* n.sp.

Fig. 70.

Derivation of the Name.—Latin *robustus*, powerful, robust, referring to the general appearance of the carapace.

Holotype.—A left female valve, No. G375 (Fig. 70A).

TYPE STRATUM AND TYPE LOCALITY.—Hemse Beds at Snoder, Gotland.

DIAGNOSIS.—*Craspedobolbina* (*Mitrobeyrichia*) sp. with a stout syllobial cusp continued backwards in a cuspidal plica the contour of which forms a straight or slightly concave line towards the extreme posterodorsal part of the syllobium. Zygal arch not very prominent, not curving down much below a line drawn forwards through the syllobial groove. Velum very markedly widened anteroventrally.

DESCRIPTION.—The lobular differentiation and the syllobial groove are deeper than in any other *Craspedobolbina* species. The velum is so extended anteroventrally in the male that its edge is often a little concave in lateral view; only along this part is it distinctly tubulous. There is an anteroventral depression. The posteroventral bend of the velar edge is rather angular, especially in the male; the female velum is generally less constricted behind the crumina than in *C. lembodes*. The granulosity is even and dense but is missing in the sulcules as well as in the sulci.

DIMENSIONS.—Hinge length–sulcal height of female valves, in microns.

Snoder: 1995–1440, 1895–1320, 1865–1300, 1850–1321, 1850–1285.

Eske: 1950–1430, 1945–1320, 1915–1300, 1895–1220, 1755–1345.

REMARKS.—This species is often very similar to *C. lembodes* but differs from it by the morphology of the cuspidal plica and the anteroventral part of the velum. The scarcity of material of adult specimens in the (Hunninge–)Amlings–Tjängdarve area makes it very difficult to distinguish objectively between the species by means of the diagnostic characters stated.

OCCURRENCE.—Hemse Beds: Snoder, Eske, Lukse, Petes, Hemmungs, ?Sandarve (females but no large tecnomorphs), ?Tjängdarve (female but no large tecnomorphs), ?Tänglings (large specimens of both sexes present; main diagnostic characters with variational trends in the direction of *C. lembodes*).

Craspedobolbina (*Mitrobeyrichia*) *cuspidulata* n.sp.

Fig. 71.

DERIVATION OF THE NAME.—Latin *cuspidulatus*, provided with small cusps, referring to the pointed lobal cusps as good diagnostics.

HOLOTYPE.—A left female valve, No. G377 (Fig. 71A).

TYPE STRATUM AND TYPE LOCALITY.—Slite Beds at Längars, Gotland.

DIAGNOSIS.—Very small *Craspedobolbina* (*Mitrobeyrichia*) sp. with very slight lobular differentiation and zygal arch curving down considerably below a line projected forwards along the faint syllobial groove. Narrow syllobium, gently drawn out into a cusp pointed very similarly to the cusp of the anterior lobe.

DESCRIPTION.—There is an almost indiscernible but constant depression below the cusp of the anterior lobe, and an equally faintly marked sulcule separates a very narrow and low anteroventral lobule. The syllobium is of the narrower type found in most populations of *C. percurrens* and in *C. clavata*, and coupled with this contracted shape of the carapace is the deeply rounded

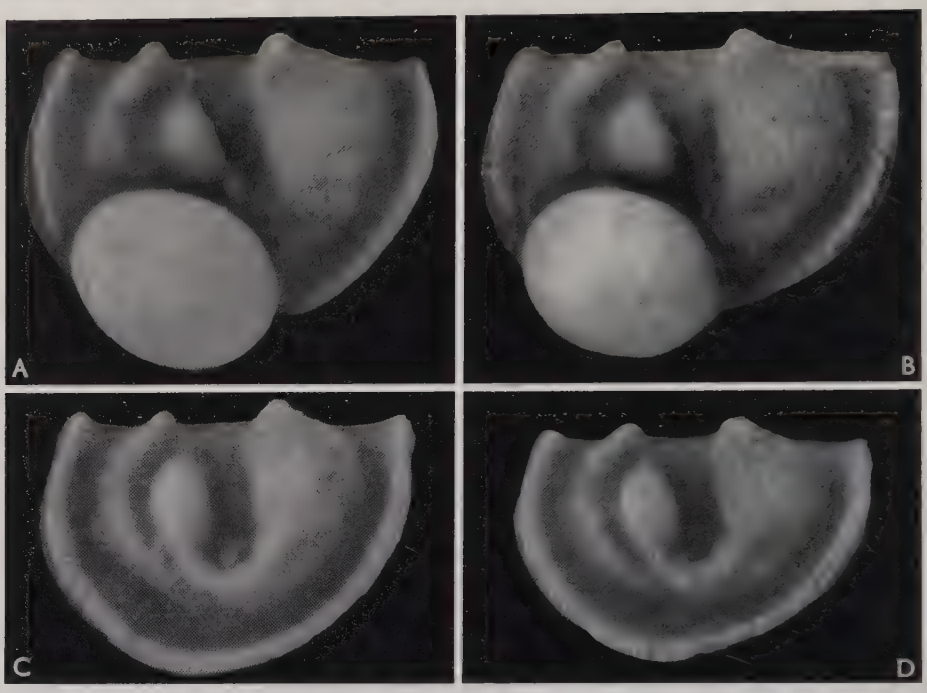


Fig. 71. *Craspedobolbina* (*Mitrobeyrichia*) *cuspidulata* n.sp., Slite Beds, Längars. A. Female valve, No. G 377 (holotype). B. Female valve, No. G 378. C. Tecnomorph, No. G 379. D. Tecnomorph, No. G 380. ×40.

but yet distinctly preplete outline of the velar edge. An anteroventral depression is present; tubules of the velum distinct only anteroventrally in some tecnomorphs. The granulation is very fine and in most samples obsolete or not preserved; the crumina is smooth.

Dimensions.—Hinge length–sulcal height of female valves, in microns:

Längars: 1320–900, 1300–840, 1280–830, 1270–920, 1280–830.

Vallstena: 1280–780, 1225–800, 1220–745, 1195–730, 1170–770.

Remarks.—This species is fairly similar to some populations of *C. percurrens* (cf. Figs. 66 and 71 on the same scale) but is readily distinguished from it by the great difference in size and the shape of the syllobial cusp.

Occurrence.—The species occurs in a well delimited area east of the main marl zone in the Slite Beds, but also west of it together with a concomitant fauna also occurring east of the marl zone: Haganäs, Fårö Skola, Längars, Kyllej, Slite I, Slite II, Enholmen, Gane, Vallstena, Nygårds, Norrbys, Gardrungs.

Subgenus *Craspedobolbina* (*Clavobolbina*) n. subg.

Derivation of the Name.—From Latin *clavus*, rudder, and the generic name *Bolbina* used in many beyrichiid compound names, referring to the very specialized female velum.

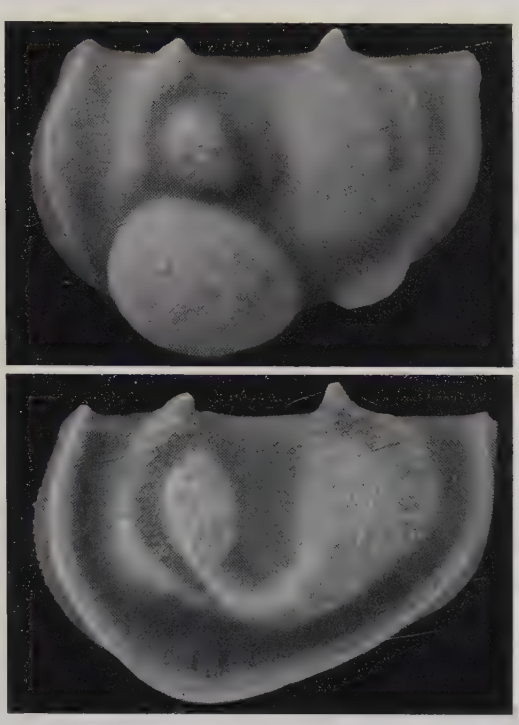


Fig. 72 A. *Craspedobolbina* (*Clavobolbina*) *acuminulata* n.sp., Slite Beds, Follingbo I. Female valve, No. G 381 (holotype). ×40.

Fig. 72 B. Same species, same locality. Male valve, No. G 382. ×40.

Type Species.—*Craspedobolbina* (*Clavobolbina*) *acuminulata* n.sp.

Species.—Only the type species.

Diagnosis.—*Craspedobolbina* sp. with female velum forming a more or less wing-like process behind the crumina from which it is separated by a considerable constriction. Syllobial cusp more or less acutely spine-shaped. A verrucose field posterodorsally on the female syllobium is separated from the rest of the syllobium by a shallow depression.

Craspedobolbina (*Clavobolbina*) *acuminulata* n.sp.

Figs. 27: 4–8, 42: 1, and 72.

1960 *Beyrichia* (*Mitrobeyrichia*) sp. A—Martinsson 1960b, Fig. 8; Pl. III, figs. 4–8; Pl. IV, fig. 1.

Derivation of the Name.—Latin *acuminulatus*, provided with a small point, referring to the shape of the syllobial cusp.

Holotype.—A left female valve, No. G381 (Fig. 72A).

Type Stratum and Type Locality.—Slite Beds at Follingbo I, Gotland.

Diagnosis.—As for the subgenus.

Description.—No distinct lobular differentiation of the anterior lobe, though there is a faint depression below the pointed cusp. Preadductorial node and zygal arch very prominent. Syllobium comparatively narrow, without a groove. Sulcus proportionally broader than in any other representative of the

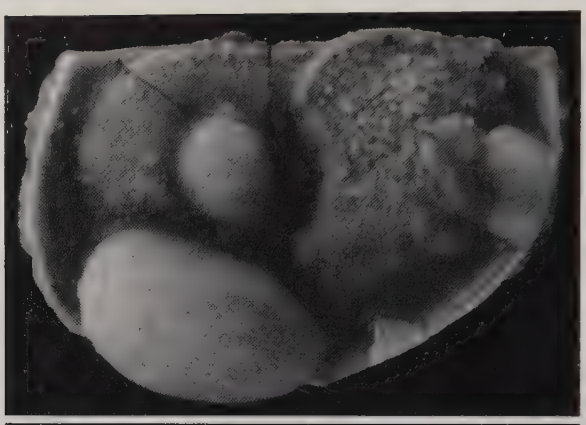


Fig. 73 A. *Craspedobolbina* (*Odoniobolbina*) *lativelata* n.sp., Halla Beds, Hörsne. Female valve, No. G 383 (holotype). × 40.

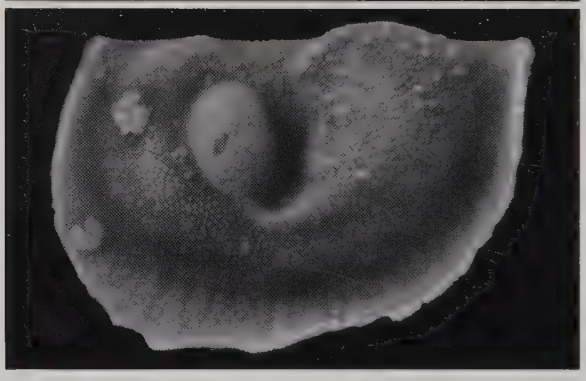


Fig. 73 B. Same species, same locality. Male valve, No. G 384. × 40.

subfamily. Anteroventral depression more marked than in other species of the genus. Velar contour pronouncedly preplete in the male; velum extended and distinctly tubulous anteroventrally; ornamental ridge along its thickened edge. The characteristic constriction of the velum in the female may in some specimens, especially if seen in strictly lateral view, be considerably less pronounced than in Fig. 72A (cf. Fig. 27: 8). Lobes in the male ornamented with an even combination of granulosity and verrucosity; females decidedly granulose only on the higher parts of the lobes; the verrucose pattern is then very distinct along an isolated, curved field posterodorsally. Acroidal processes occur even on adult right valves.

Dimensions.—Hinge length–sulcal height of female valves from the type locality; in microns: 1450–865, 1440–905, 1370–845, 1365–800, 1350–810 (see also dispersion diagram, Fig. 75).

Remarks.—The species is especially interesting because of the influences of sexual dimorphism also on carapace parts other than the crumina. Even in specimens with incomplete cruminal metamorphosis (Fig. 27: 4) there is a tendency towards a differentiation of the verrucose pattern.

Occurrence.—Slite Beds: Alby, Puttarsjaus, Längars, Slite I, Gane, Norrbys, Follingbo I, Follingbo II, Follingbo III.

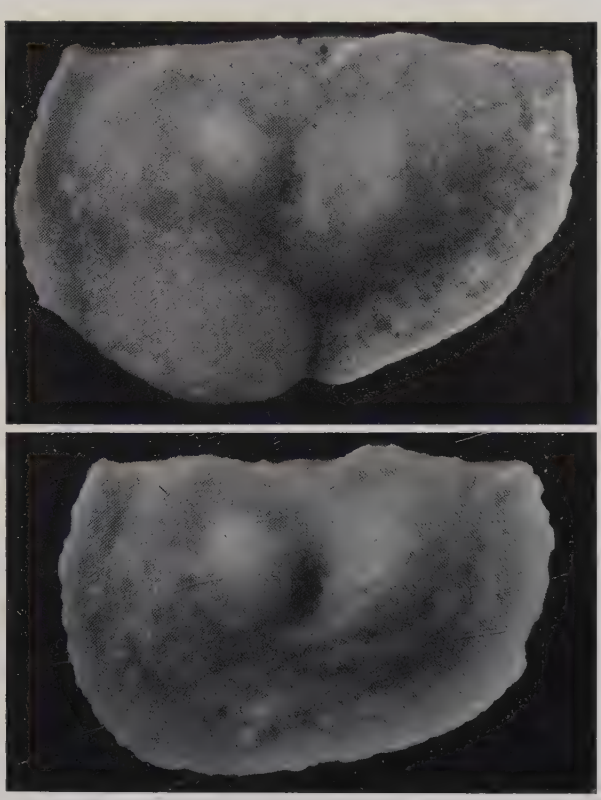


Fig. 74 A. *Craspedobolbina* (*Odoniobolbina*) cf. *lativelata* n.sp., Klinteberg Beds, Hunninge. Female valve, No. G 385. ×40.

Fig. 74 B. Same species, same locality. Tecnomorphic valve, No. G 386. ×40.

Subgenus *Craspedobolbina* (*Odoniobolbina*) n. subg.

Derivation of the Name.—Greek ὀδόντιον, sail, and the generic name *Bolbina*, referring to the very wide velum.

Type Species.—*Craspedobolbina* (*Odoniobolbina*) *lativelata* n.sp.

Species.—Only the type species.

Diagnosis.—*Craspedobolbina* sp. with very wide velum, cristate cuspidal plica on the syllobium, and an almost obsolete anterior lobe.

Craspedobolbina (*Odoniobolbina*) *lativelata* n.sp.

Fig. 73; *C.* (*O.*) cf. *lativelata* Fig. 74.

Derivation of the Name.—Latin *latus*, wide, and *velatus*, provided with a velum.

Holotype.—A left female valve, No. G383 (Fig. 73A).

Type Stratum and Type Locality.—Halla Beds at Hörsne, Gotland.

Diagnosis.—As for the subgenus.

Description.—Only a small cuspidal elevation marks the existence of the anterior lobe; from the very large preadductorial knob the carapace wall is

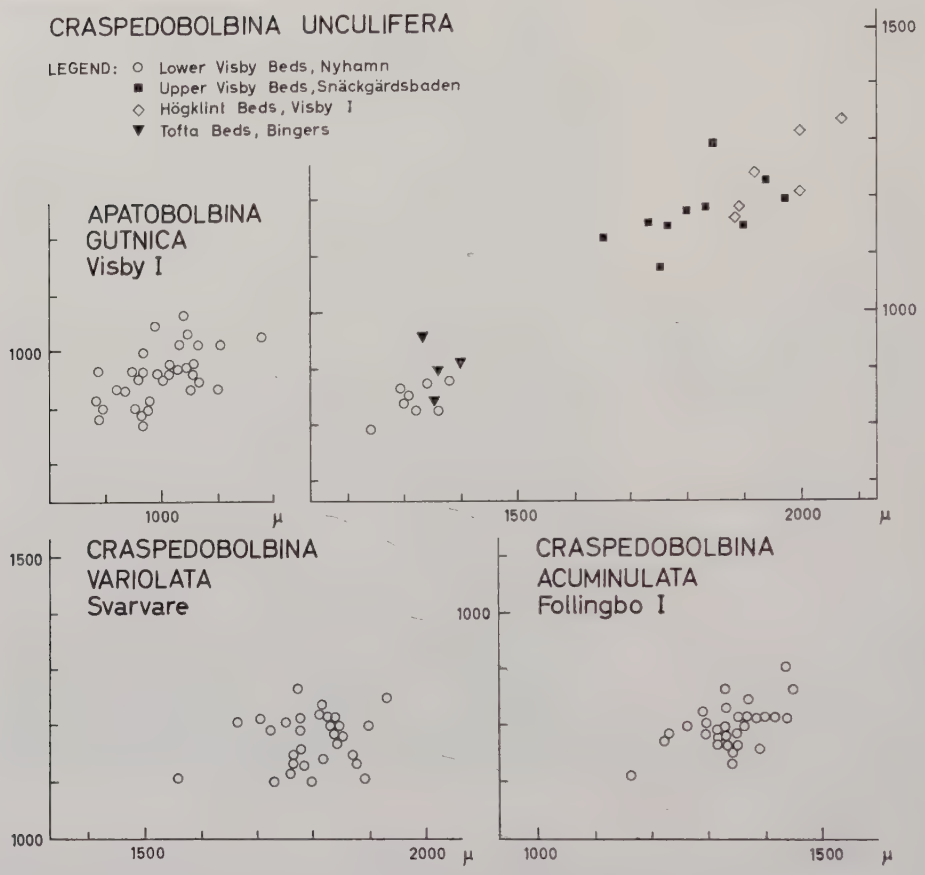


Fig. 75. Size dispersion of female specimens (right and left valves not differentiated, hinge length *versus* height over the sulcal region) in some representative *Craspedobolbinae*.

gently curved towards the base of the velum; the prenodal sulcus is, consequently, very shallow. Adductorial sulcus narrow; zygal ridge not very prominent; syllobium broad without a distinct groove. Velum very wide but tapering towards the hinge corners; there is an ornamental ridge on the outside of the velum at some distance from its thin edge. More or less distinct tubulosity along the greater part of the male velum; tubulosity very indistinct in the female; the egg-shaped crumina does not cause a very pronounced constriction of the velum. Non-velar parts of the carapace granulose with a superimposed verrucosity; a fine granulation even reaches down into the adductorial sulcus; crumina granulo-striate lengthwise.

Dimensions.—Hinge length–sulcal height of female valves from the type locality: 1765 μ – 1210 μ, 1710 μ – 1145 μ, 1675 μ – 1165 μ, 1645 μ – 1230 μ.

Occurrence.—Halla Beds: Hörsne. Though not particularly rare at this locality, the species is represented only by four measurable female specimens.

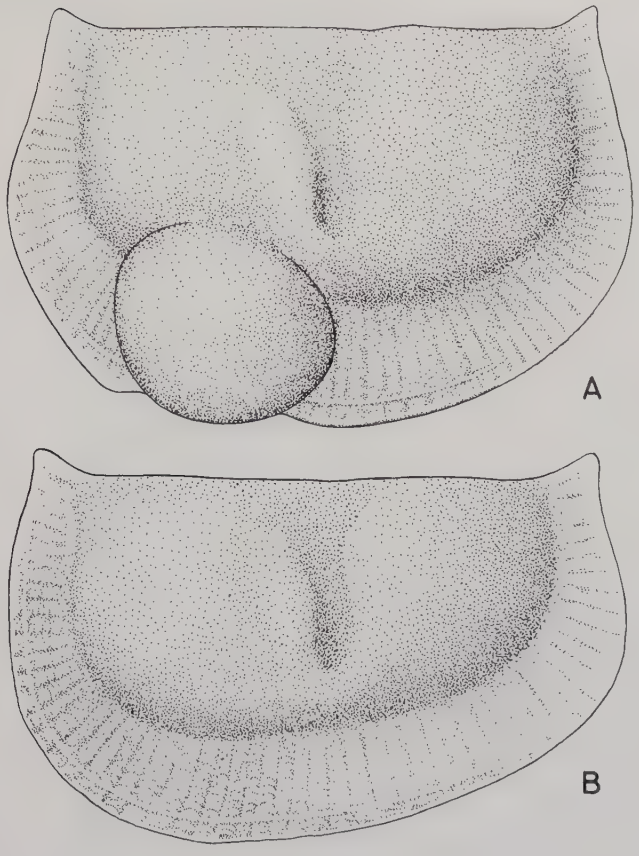


Fig. 76. *Hyrsinobolbina* n.g. Reconstructive drawing based on specimens of *Hyrsinobolbina hyrsinensis* n.sp. ×40. A. Female. B. Male.

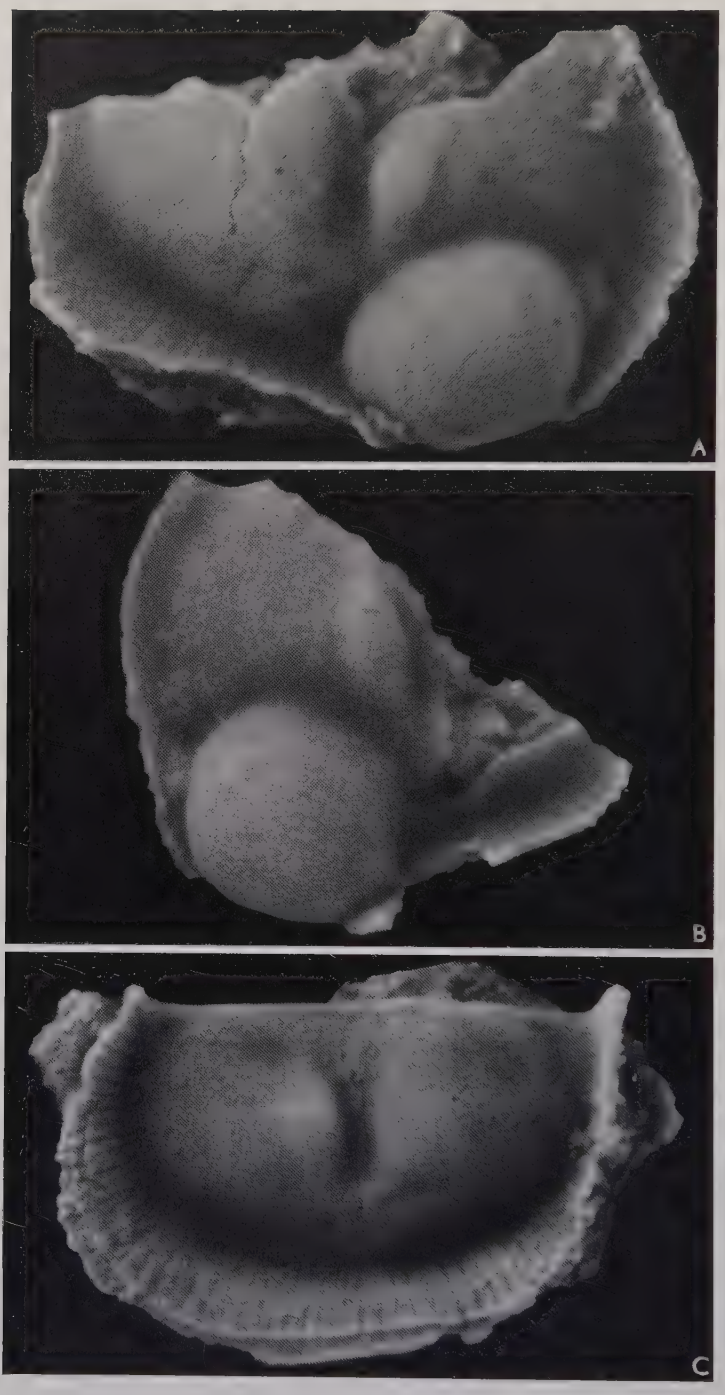
Material from the Slite and Klinteberg Beds.—*Craspedobolbina* cf. *lativelata* has been found at Norrbys, Follingbo III, and Slite I in the Slite Beds (small tecnomorphs) and at Hunninge in the Klinteberg Beds (Fig. 74). The material from the latter locality is very badly preserved in a matrix very different from the rocks at Hörsne which makes comparison very difficult. The female figured shows a zygal arch not influenced by the crumina, but another specimen from the same locality shows the normal obsoletion of this arch.

Genus *Hyrsinobolbina* n.g.

Fig. 76.

Derivation of the Name.—Latinized from the stem *Hyrsin-* in a Medieval spelling of the parish name of Hörsne, and the generic name *Bolbina*.

Type Species.—*Hyrsinobolbina hyrsinensis* n.sp.



Female valve, No. G 387 (holotype).

Female valve, No. G 388.

Tecnomorphic valve, No. G 389.

Fig. 77. *Hyrsinobolbina hyrsinensis* n.sp., Halla Beds, Hörsne. × 40.

Fig. 78. *Hyrsinobolbina hyrsinensis* n.sp., Halla Beds, Hörsne. Same specimen as Fig. 77 A (No. G 387, the holotype) in oblique ventral view. ×40.

Species.—Only the type species.

Diagnosis.—*Craspedobolbininae* with a ridge below the dolonoid scar on the crumina. Lobation consisting of an almost obsolete preadductorial node, connected with the syllobial part of the valve by a likewise almost obsolete zygal ridge below a narrow sulcus at mid-length of the valve. Velum broad and tubulous from the anterior to the posterior hinge corner.

Hyrsinobolbina hyrsinensis n.sp.

Figs. 77 and 78.

Derivation of the Name.—Latin *Hyrsinensis*, coming from Hörsne, derived from the same stem as the generic name.

Holotype.— A fragmentary right female valve, No. G 387 (Figs. 77 A and 78).

Type Stratum and Type Locality.—Halla Beds at Hörsne, Gotland.

Diagnosis.—Same as for the genus.

Description. –Lateral side of valve flattened, except for features mentioned in the diagnosis. Velum very broad and tubulous all around; the tubules at the hinge corners, protruding in anterodorsal and posterodorsal direction, respectively, terminate the velum abruptly. The tubules are comparatively narrow and are finely wrinkled transversally like the tubules in *Apatobolbina*; there is, however, an ornamental crest along the velar edge as in *Craspedobol-*

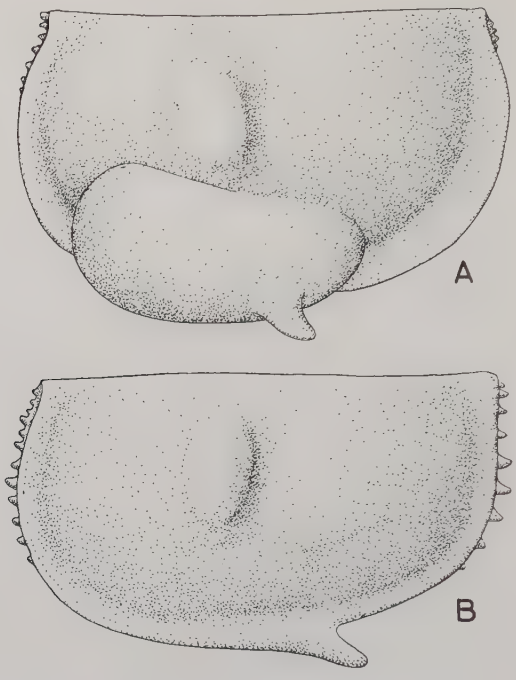


Fig. 79. *Aitilia* n.g. Drawing based on *Aitilia calcarata* n.sp. ×45. A. Female. B. Male.

bina, and the velum formed a persistent ridge as in this genus during the metamorphosis. The velum encroaches to some extent onto the crumina, parallel to this ridge. The vertical marginal frill is broad, not divided into two crescent-shaped portions as in *Craspedobolbina* spp.; the covering frill is more distinctly tubulous than the vertical one.

Dimensions.—Hinge length of a female valve ca. 1995 μ, height over the adductorial sulcus 1530 μ.

Occurrence.—Halla Beds at Hörsne, Gotland. Very rare; the material consists of three fragmentary female specimens and some tecnomorphs; the best specimens are figured here.

Genus *Aitilia* n.g.

Fig. 79.

Derivation of the Name.—Latin *Aitilius*, coming from Etelhem, derived from the stem *Aitil-* in a Medieval spelling of this parish name.

Type Species.—*Aitilia calcarata* n.sp.

Species.—*Aitilia calcarata* n.sp.
Aitilia calcarulata n.sp.
Aitilia hyrsinicola n.sp.

Diagnosis.—Coarsely or finely punctate *Craspedobolbininae* with a flattened

or narrow velum and a posteroventrally directed spur on a long, cucumber- or sausage-shaped crumina. Male velum very narrow or missing behind the spur. The only lobal feature is a preadductorial node in front of a narrow adductorial sulcus; the node is fused with the anterior part of the valve wall.

Aitilia calcarata n.sp.

Fig. 80A–C, E–F.

Derivation of the Name.—Latin *calcaratus*, provided with a (normally large) spur.

Holotype.—A left female valve, No. G 390 (Fig. 80A and E).

Type Stratum and Type Locality.—Hemse Beds at Tänglings, Gotland.

Diagnosis.—*Aitilia* sp. with broad velum in the female and a cucumber-shaped crumina, tapering posteriorly; calcarine spine forming a long spur near the posterior end of the crumina.

Description.—The part of the carapace wall corresponding to the anterior lobe and the syllobium bulging only very slightly; adductorial complex as in the generic diagnosis; a faint syllobial groove, subparallel to the base of the velum, present in the tecnomorphs. Velum in the female broad, indistinctly tubulous, tapering towards the cardinal corners; separated on the crumina from the very oblique dolonoid scar. There is a very low toric ridge near the base of the velum; no ornamental thickenings along the velar edge. Male velum much narrower, drawn out into a spur behind the sulcus; behind the spur it may be marked as a bend for some distance but soon becomes obsolete. Ornamentation a combination of granulosity and a coarse punctation; in the female the punctation dominates over the granulosity which is visible only locally. Crumina longitudinally striate. Vertical marginal structures dissolved into rows of spines or tubercles, the covering structure is on the left valve; acroidal processes even in rather large left valves.

In young moult stages the calcarine spine is a completely dominant feature; other parts of the velum are marked only as ridges or bends; acroidal processes often very dominant.

Dimensions.—Hinge length–sulcal height of female specimens. Tänglings: 1465 μ – 865 μ, 1430 μ – 900 μ. Hunninge: 1400 μ – 930 μ.

Remarks.—The homogeneity of the species can be drawn into question, and the male is very imperfectly known. The limited material suggests the following differences in the material from Hunninge (Hemse and Klinteberg Beds, respectively) as compared with the material from Tänglings: Crumina less markedly tapering posteriorly, dolonoid scar longer and less oblique; less separated from the velum; marginal spinules coarser (Fig. 80F); tecnomorphic velum slightly broader.

This species is easily distinguished from *A. calcarulata* and *A. hyrsinicola* by the shape of the crumina, the width of the velum, and the length of the calcarine spine.

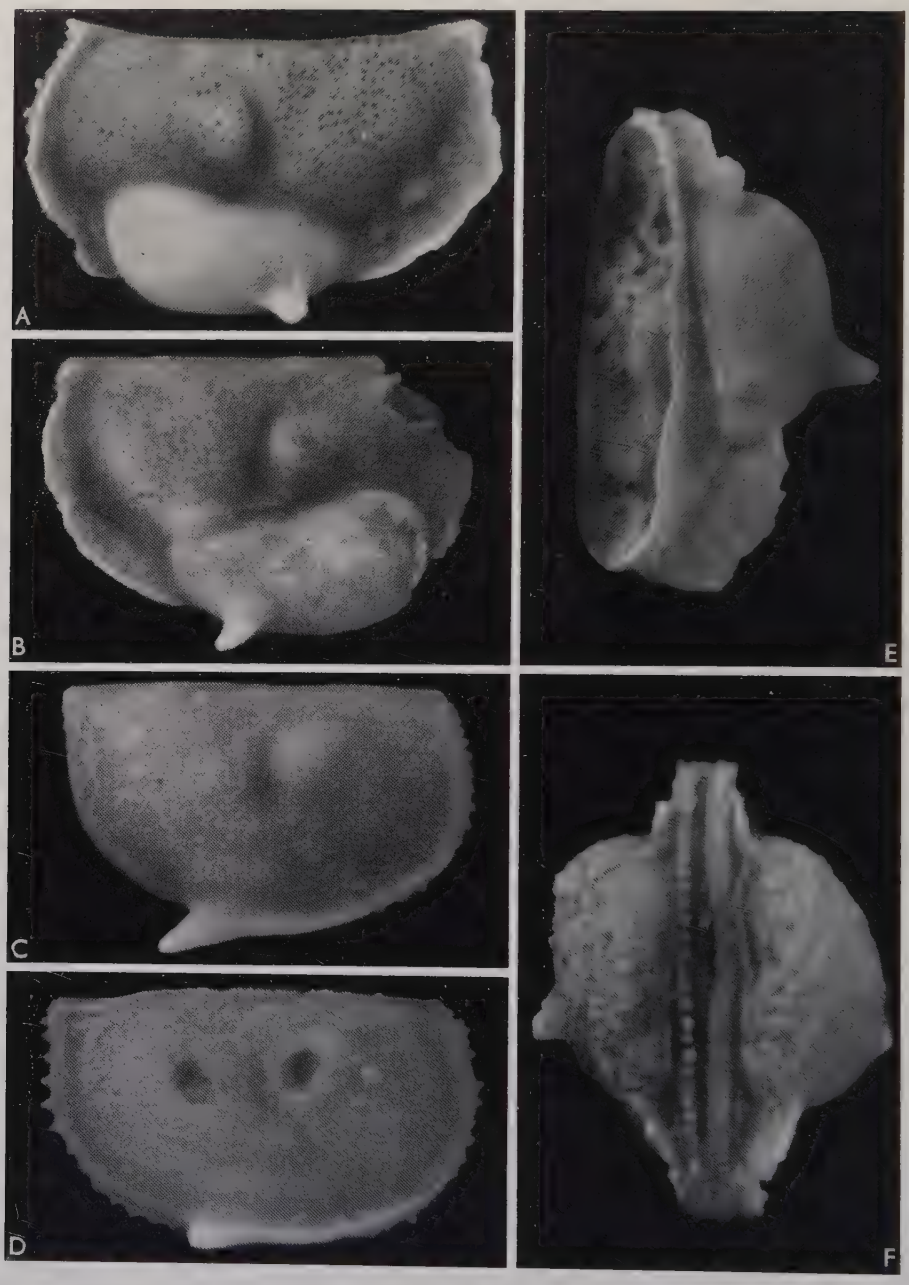


Fig. 80. A–C, E–F. *Aitilia calcarata* n.sp. A–B and E. Hemse Beds, Tänglings. C and F. Klinteberg Beds, Hunninge. ×40. A and E. Female valve lateral and ventral (anterior end up) view. No. G 390 (holotype). B. Female valve, No. G 391. C. Tecnomorphic valve, No. G 392. F, Female valve in ventral view (anterior end up), No. G 394. D. *Aitilia* cf. *calcarulata* n.sp., Klinteberg Beds, Hunninge, No. G 393 (cf. Fig. 89 D). ×40.

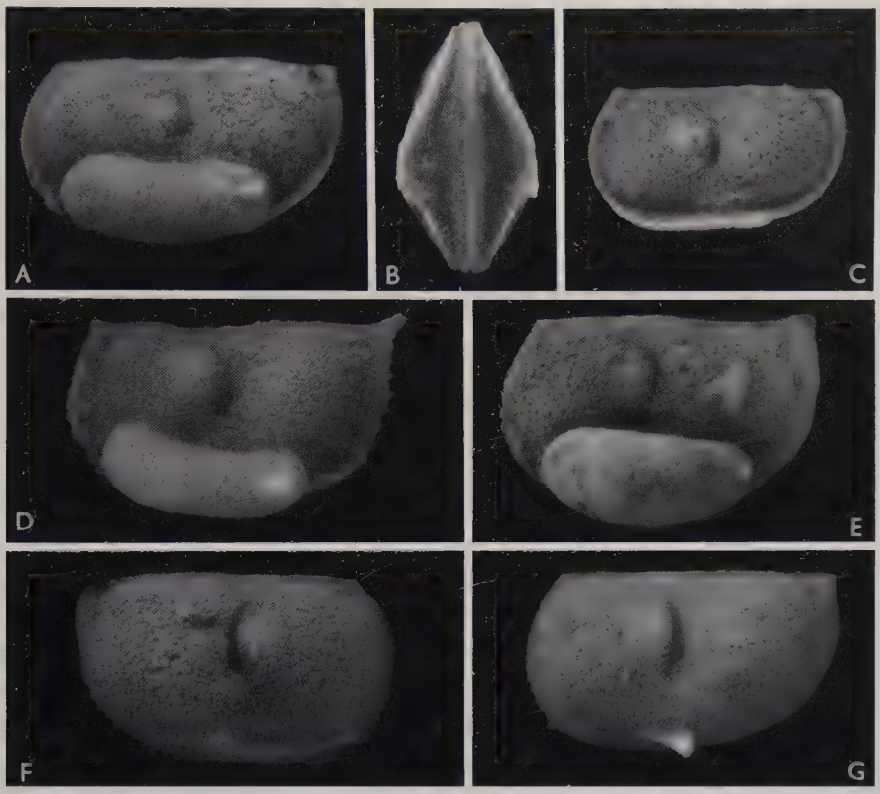


Fig. 81. A–C. *Aitilia calcarulata* n.sp., Eke Beds, Lau Backar. ×30. A. Female valve, No. G 395 (holotype). B–C. Tecnomorphic carapace in ventral (anterior end up) and lateral view, No. G 396. D. *Aitilia* cf. *calcarulata* n.sp., Klinteberg Beds, Hunninge, female valve, No. G 397. ×30. E–G. *Aitilia hyrsinicola* n.sp. Halla Beds, Hörsne. ×30. E. Female valve, No. G 398 (holotype). F–G. Male valves, Nos. G 399 and G 400.

Occurrence.—Klinteberg Beds: Hunninge (2 females and a few tecnomorphs, one of which is probably adult). Hemse Beds: Tänglings (3 females and a few small tecnomorphs).

Aitilia calcarulata n.sp.

Fig. 81 A–D.

Derivation of the Name.—Latin *calcarulatus*, provided with a small spur.

Holotype.—A left female valve, No. G 395 (Fig. 81 A).

Type Stratum and Type Locality.—Eke Beds at Lau backar, Gotland.

Diagnosis.—*Aitilia* sp. with narrow velum in both sexes and a long, sausage-shaped crumina; calcarine spine developed as a short spur near the posterior end of the crumina. Sparse surface punctation.

Description.—Lobation as in the preceding species. Velum consisting of a very narrow flange, without any visible tubulosity; crumina as in specific

diagnosis, equally thick from end to end. The tecnomorphic velum is united with the calcarine spine in a broadly triangular flap. Finer and sparser punctation than in the preceding and following species. Marginal structures on the whole very similar to these structures in the preceding species. Acroidal processes even in adult left valves.

Dimensions.—Hinge length–sulcal height of female valves from the type locality: 1330 μ – 925 μ, 1305 μ – 1000 μ, 1250 μ – 920 μ.

Remarks.—This species is very similar to *C. hyrsinicola* n.sp. but differs from it by the width of the velum, the size of the calcarine spine, and the density of the punctation.

Occurrence.—Eke Beds: Lau backar (rare).

A. cf. *calcarulata* occurs rarely in the Klinteberg Beds at Hunninge (Figs. 80D and 81D) and in the Hemse Beds at Sigvalde (one tecnomorph).

Aitilia hyrsinicola n.sp.

Fig. 81E–G.

Derivation of the Name.—Latin *Hyrsinicola*, native of Hörsne.

Holotype.—A left tecnomorphic valve, No. G398 (Fig. 81E).

Type Stratum and Type Locality.—Halla Beds at Hörsne, Gotland

Diagnosis.—*Aitilia* sp. with very narrow velum in both sexes and a long sausage-shaped crumina; a very small calcarine tubercle near the posterior end of the crumina, corresponded to in the male by a short spine projecting from the velar ridge. Dense surface punctation.

Description.—Lobation as in the preceding species; a syllobial groove can be traced. Velum in both sexes not more than a ridge; crumina thickest at about mid-length; the calcarine spine is very small in both sexes; when at its largest it draws out the male velar ridge into a small triangular flap.

Dimensions.—Hinge length–sulcal height of female valves from the type locality: 1365 μ – 845 μ, 1350 μ – 930 μ, 1345 μ – 1065 μ, 1265 μ – 1010 μ.

Remarks.—Differential characters in comparison with *A. calcarulata* given above.

Occurrence.—Halla Beds: Hörsne. Yet another species, *A.* aff. *hyrsinicola*, with a somewhat shorter crumina without a calcarine spine in the female, is known from very few specimens at Slite II in the Slite Beds.

Genus *Hamulinavis* n.g.

Fig. 82.

Derivation of the Name.—A diminutive of Latin *hamus*, hook, and *navis*, referring to the acroidal processes suggestive of the protruding stems of a ship.

Type Species.—*Hamulinavis pirulifera* n.sp.

Species.—Only the type species.

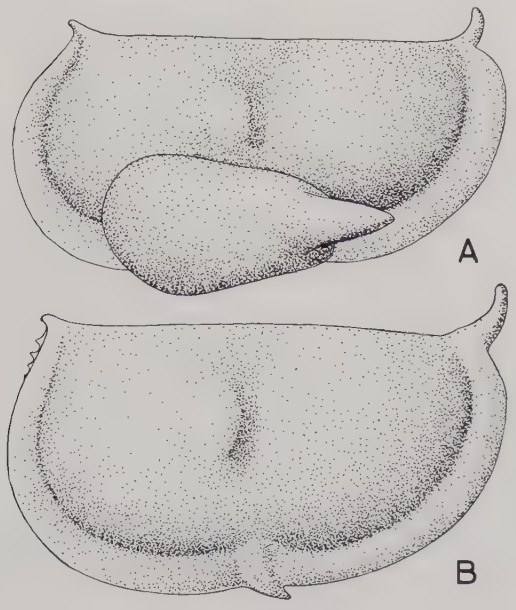


Fig. 82. *Hamulinavis* n.g. Drawing based on *Hamulinavis pirulifera* n.sp. ×40. A. Female. B. Male.

Diagnosis.—Smooth *Craspedobolbininae* with a convex, non-tubulous, broad velum. A calcarine spine deflects the male velum below the sulcus and forms a spur near the posterior end of the crumina, pointing in a posterolateral direction. The only lobal feature is a preadductorial node in front of a narrow and small adductorial sulcus; the node is fused with the anterior part of the valve wall.

Hamulinavis pirulifera n.sp.

Figs. 83 and 84A.

Derivation of the Name.—Latin *pirulifer*, carrying a small pear, referring to the shape of the crumina, suggestive of a pear with stalk.

Holotype.—A right female valve, No. G401 (Figs. 83A and 84A).

Type Stratum and Type Locality.—Eke Beds at Lau Backar, Gotland.

Description.—Lobation as in the diagnosis; there is a very faint syllobial groove, and the zygal connections with the syllobial part of the carapace can hardly be traced. Outer side of the velum smooth and convex; velum gently tapering towards the anterior hinge corner, broadly rounded at the posterior corner. Crumina long, with a rounded anterior portion, set off just below the sulcus from the tapering posterior portion with the spine (see the Figures). The left valve has proportionally larger acroidal processes than any other adult ostracode; the posterior process is curved in a forward direction.

Ventral side of the crumina with an oblique dolonoid scar; velum encroaching

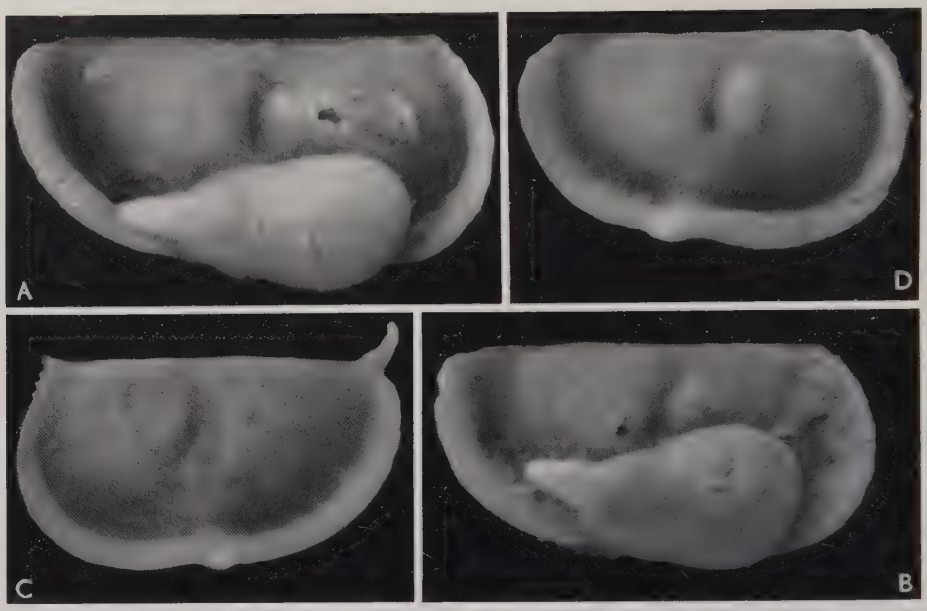


Fig. 83. *Hamulinavis pirulifera* n.sp., Eke Beds, Lau Backar. ×40. A. Female valve, No. G 401 (holotype). B. Female valve, No. G 404. C. Tecnomorph, No. G 403. D. Tecnomorph, No. G 402.

onto the crumina, not constricted by the cruminal metamorphosis. Vertical marginal structure consisting of densely spaced spinules.

Dimensions.—Hinge length–sulcal height of female valves from Lau Backar: 1360 μ – 845 μ, 1350 μ – 865 μ, 1300 μ – 785 μ, 1245 μ – 785 μ.

Occurrence.—Eke Beds: Lau backar.

One tecnomorph of *H.* cf. *pirulifera* has been found at Tänglings in the Hemse Beds.

Genus *Mesomphalus* Ulrich & Bassler 1913

Type Species.—*Mesomphalus hartleyi* Ulrich & Bassler 1913.

Species.—Only the type species.

Diagnosis.—*Craspedobolbininae* with a flange-like velum and a sausage-shaped crumina largely incorporated with the carapace wall. Dolonoid scar developed as a long fissure parallel to the margin of the valve. Preadductorial node not set off by a prenodal sulcus, connected with the syllobium by a zygal arch; distinct horizontal groove and dorsal plica on the syllobium. Surface granulose, finely punctate.

Remarks.—The delimitation of the genus *Clintiella* n.g. makes a regrouping based solely on figures necessary for some species referred to *Mesomphalus* (see below); it is impossible to group *Clintiella hyrsiniana* together with *Clintiella*

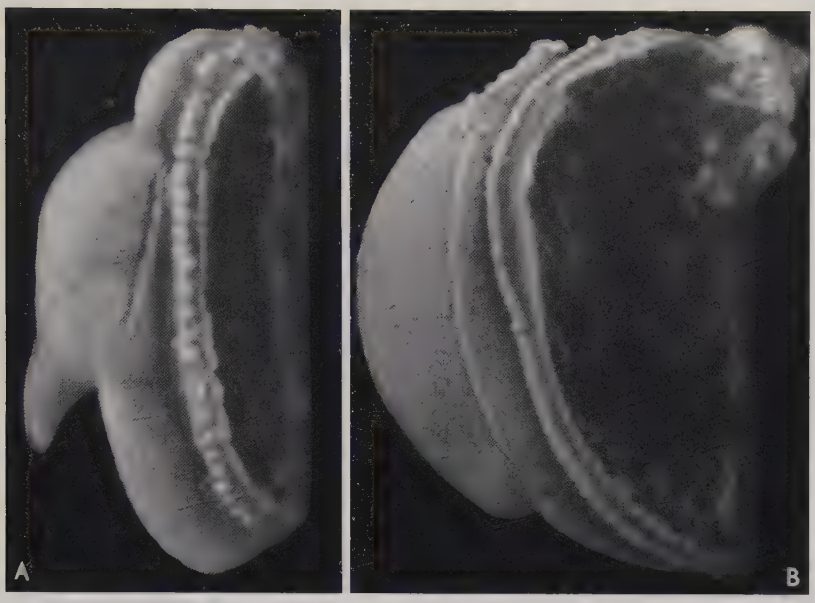


Fig. 84. Dolonoid scars in *Hamulinavis* and *Clintiella*. A. *H. pirulifera* n.sp., Eke Beds, Lau Backar, No. G 401 (same specimen, the holotype, as in Fig. 83 A.) × 50. B. *C. hyrsiniana* n.sp., No. G 405. × 40.

hunningiana without at the same time treating *Mesomphalus rhomboidalis* Swartz & Whitmore. The ventral morphology of the *Mesomphalus* species described by Swartz & Whitmore 1956 is not known. In any case *Mesomphalus hartleyi* differs from *Clintiella* by having a crumina which is clearly set off from the wall of the valve, but it cannot be discerned with full certainty from the only good figures published (Kesling & Rogers 1957 Pl. 130, Fig. 15, etc.; cf. Ulrich & Bassler 1913, Pl. XCVI, fig. 1) whether *Mesomphalus* has also the characteristic crest inside the scar which is found in *Clintiella*. With the present evidence it is necessary to include the American Silurian species referred to *Mesomphalus* in *Clintiella*.

Genus *Clintiella* n.g.

Fig. 85.

Derivation of the Name.—Feminine diminutive of an adjective *Clintius*, inhabitant of the parish of Klinte.

Type Species.—*Clintiella hunningiana* n.sp.

Species.—*Clintiella hunningiana* n.sp.
Clintiella bingeriana n.sp.
Clintiella hyrsiniana n.sp.
Mesomphalus rhomboidalis Swartz & Whitmore 1956
Mesomphalus striatellus Swartz & Whitmore 1956

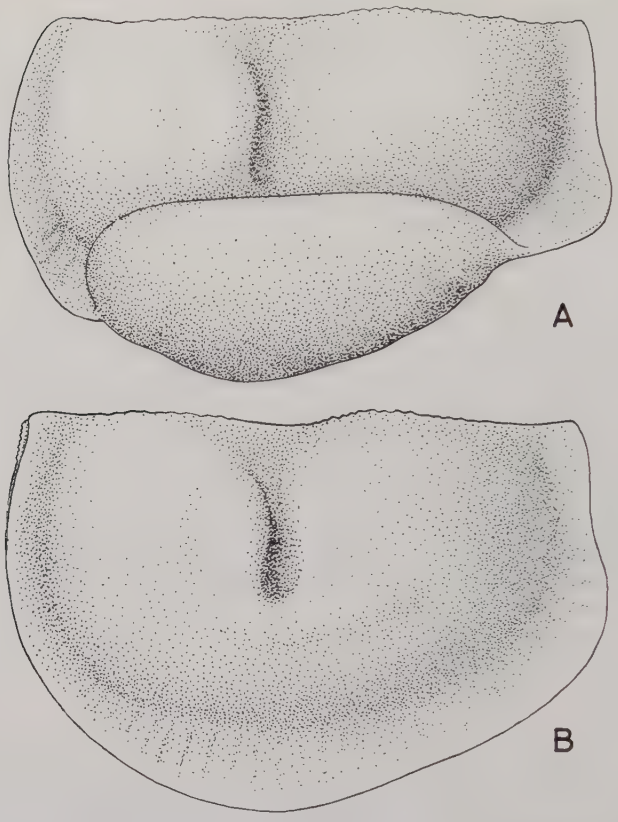


Fig. 85. *Clintiella* n.sp. Drawing based on specimens of *Clintiella hunningiana* n.sp. ×40. A. Female. B. Male.

Diagnosis.—*Craspedobolbininae* with a long crumina, distinctly set off from the carapace wall and still largely consisting of velar elements. Long dolonoid scar as a furrow outside a thin but sharp ridge. Narrow sulcus curving round the almost obsolete preadductorial node; syllobial groove present.

Remarks.—As seen in lateral view, the *Clintiella* species are immediately associated with *Craspedobolbininae* of the spurred type, with a long crumina. The dolonoid scar, however, is very long and very specialized; it is possible that the formation of the dolonoid pouch and the insertion of the flap have already been reduced to a simple plication of the inner velar layer in the corresponding region. In the extreme case, as shown in Fig. 84 B, there is a crumina strikingly similar to that in the *Treposellinae*, with two bridges separating the anterior and posterior portions of the velar edge from the ridge along the ventral base of the crumina. It may be of phylogenetic significance that a new genus consisting of the two species *Bolbiprimitia limbata* and *B. teresaccula* (see Swartz & Whitmore 1956) is so perfectly intermediate between *Clintiella* and *Bolbiprimitia* and associated treposelline genera that it is impossible to place it into either subfamily without a special investigation of their ventral morphology.

Clintiella hunningiana n.sp.

Figs. 86 A–D.

Derivation of the Name.—Latin *Hunningianus*, associated with Hunninge, referring to the type locality.

Holotype.—A right female valve, No. G406 (Fig. 86A).

Type Stratum and Type Locality.—Klinteberg Beds at Hunninge, Gotland.

Diagnosis.—*Clintiella* sp. with a very wide velum not encroaching onto the crumina.

Description.—Lobation as in generic diagnosis; the syllobium has a faintly marked groove and a very low dorsal ridge. The velum is tubulous all around with a widened portion posteroventrally and tapering towards the hinge corners; the tubules are flattened and not separated by particularly distinct depressions. The crumina is long, being thickest at about one third of its length from the anterior end; especially posteriorly its character of an inflation piercing along the velar fold is evident. A line drawn from the anterior to the posterior portion of the velar edge passes considerably outside (i.e. distally of) the dolonoid scar. Carapace coarsely granulose, with no considerable difference between the sexes.

Dimensions.—Hinge length–sulcal height of female valves:

Hunninge 1730 μ – 1265 μ. Slite II: 1775 μ – 1320 μ.

Remarks.—The species is easily distinguished from other species of the genus by its broad velum and the site of the dolonoid scar.

Occurrence.—Slite Beds: Slite II. Klinteberg Beds: Hunninge. (There are indeterminable small tecnomorphs of *Clintiella* also at two other localities in the Slite Beds: Norrbys and Follingbo III).

Clintiella bingeriana n.sp.

Figs. 86 E–G.

Derivation of the Name.—Latin *Bingerianus*, associated with Bingers, referring to the type locality.

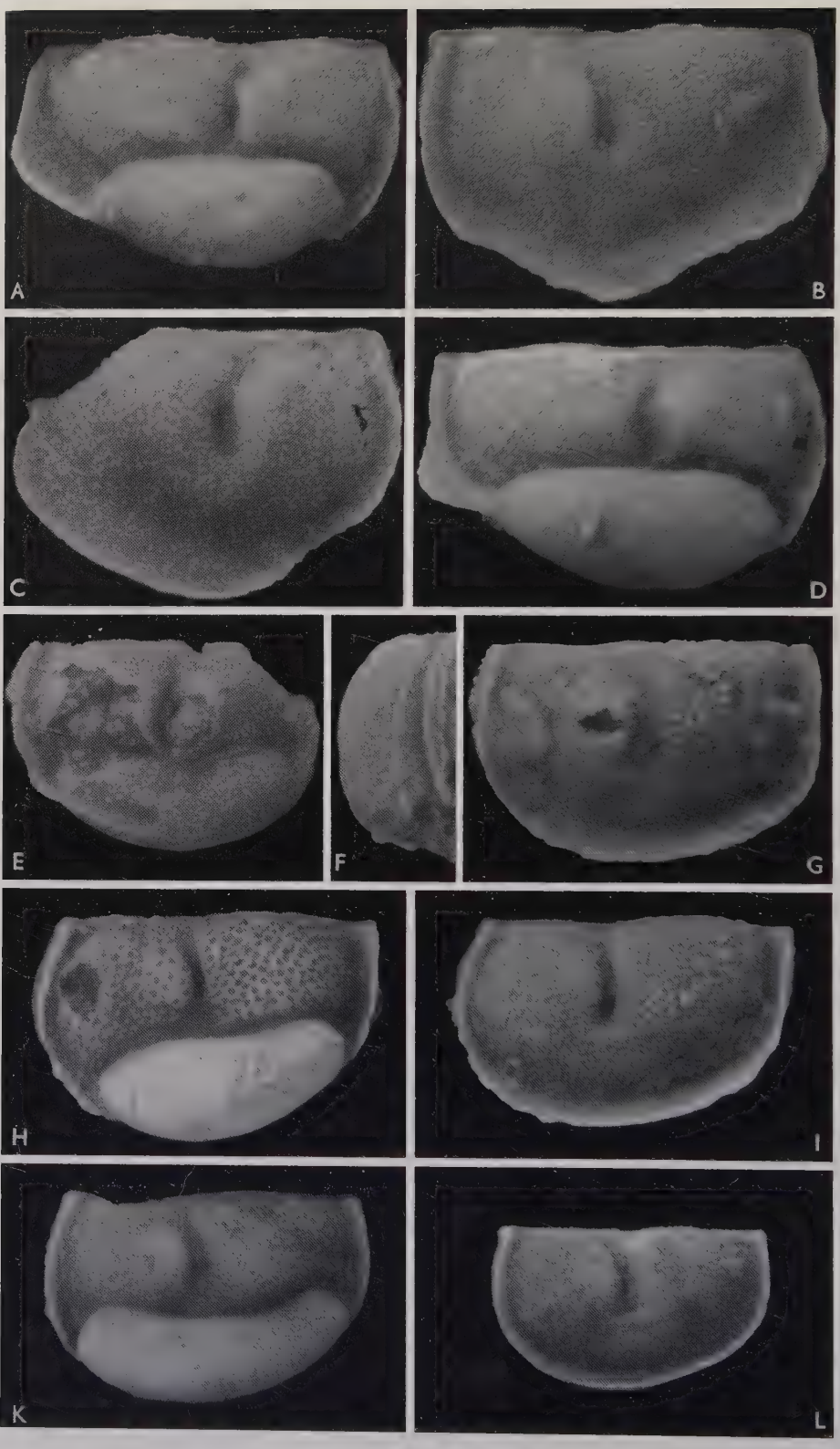
Holotype.—A right, somewhat damaged female valve, No. G410 (Fig. 86E).

Type Stratum and Type Locality.—Tofta Beds at Bingers, Gotland.

Diagnosis.—*Clintiella* sp. with a medium-wide velum the posterior portion of which is continued as a ridge lateroventrally on the posterior half of the crumina.

Description.—Lobation as in generic diagnosis; syllobial groove not very distinct. Velum tubulous, tapering towards the hinge corners; crumina thickest below the preadductorial node. Coarsely granulose, especially the male. A fine reticulation is sometimes to be seen on the crumina.

Dimensions.—Hinge length–sulcal height of the holotype: ca. 1560 μ (reconstructed) – 1120 μ.


A
B
C
D
E
F
G
H
I
K
L

Remarks.—The velar ridge on the crumina distinguishes this species from the following.

Occurrence.—Tofta Beds: Bingers (very rare).

Clintiella hyrsiniana n.sp.

Figs. 40E, 84B, and 86H–I.

Derivation of the Name.—Latin *Hyrsinianus*, associated with Hörsne, referring to the type locality.

Holotype.—A left female valve No. G413 (Fig. 86H).

Type Stratum and Type Locality.—Halla Beds at Hörsne, Gotland.

Diagnosis.—*Clintiella* sp. with a narrow velar frill; dolonoid scar separated from the velar edge only by narrow bridges.

Description.—Lobation as in the generic diagnosis; a thin callus is present above the shallow syllobial groove. Velum tapering towards the cardinal corners; its tubulosity can be observed in the male. Crumina widest below the sulcus; the ventral features mentioned in the diagnosis are seen in Fig. 84B. Female ornamentation a coarse punctation or reticulation with granules centrally in the puncta or meshes. Male ornamentation consisting of a very coarse granulosity as in the preceding species.

Dimensions.—Hinge length–sulcal height of female valves from Hörsne: 1730 μ – 1225 μ, 1665 μ – 1250 μ, 1630 μ – 1265 μ, 1595 μ – 1250 μ.

Remarks.—This species is very similar to *C. rhomboidalis* from the Silurian Decker Limestone of New Jersey but has not the deep syllobial groove found in that species; the velum in *C. hyrsiniana* is also noticeably broader.

Occurrence.—Hamra Beds: Hörsne.

Clintiella cf. *hyrsiniana*

Figs. 41 and 86K–L.

Remarks.—Without knowing the variation of the preceding species from more than one locality it seems possible to distinguish the material from the Eke Beds at Lau Backar as a separate species. It has, however, a relatively longer, more typically sausage-shaped crumina, and the bridges between the portions of the velum and the ridge inside the dolonoid scar are very little marked. The velum is also relatively narrower than in the Hörsne material. The ornamentation shows even larger differences between the sexes than the Hörsne material; every mesh in the reticulation has a small granule in the centre as in *Bolbiprimitia* (cf. p. 77).

Fig. 86 (opposite page). A–D *Clintiella hunningiana* n.sp. A from the Klinteberg Beds at Hunninge, B–D from the Slite Beds at Slite II. ×30. A. Female valve, No. G 406 (holotype). B–C. Male valves, RM Nos. Ar 26140:3, and Ar 26140:4. D. Female valve, RM No. Ar 26140:2. E–G. *Clintiella bingeriana* n.sp., Tofta Beds, Bingers. ×30. E. Female valve, No. G 410 (holotype). F. fragment of a valve showing the crumina in ventral view, No. G 411. G. Male valve, No. G 412. H–I. *Clintiella hyrsiniana* n.sp., Halla Beds, Hörsne. ×30. H. Female valve, No. G 413 (holotype). I. Male valve, No. G 414. K–L. *Clintiella* cf. *hyrsiniana* n.sp., Eke Beds, Lau Backar. ×30. K. Female valve, No. G 415. L. Tecnomorphic valve, No. G 416.

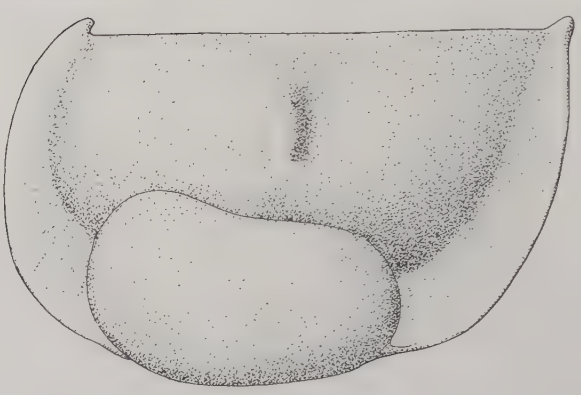


Fig. 87. *Barymetopon* n.g. Reconstructive drawing based on specimens of *Barymetopon infantile* n.sp. The tecnomorphs of this species are not known. ×60.

Genus *Barymetopon n.g.*

Fig. 87.

Derivation of the Name.—From Greek βαρύς, heavy, and μέτωπον, front, referring to the proportions of the preadductorial part of the carapace.

Type Species.—*Barymetopon infantile* n.sp.

Species.—Only the type species.

Diagnosis.—*Craspedobolbininae* with a broad velum inflated into a cylindroidal crumina the larger part of which is situated in front of a line through the sulcus. Small preadductorial node indistinctly marked in front of an almost pit-shaped, narrow sulcus.

Barymetopon infantile n.sp.

Fig. 88.

Derivation of the Name.—Latin *infantilis*, child-like, referring to the suggestively larval morphology of the species.

Holotype.—A right female valve, No. G407 (Fig. 88A).

Type Stratum and Type Locality.—Lower Visby Beds at Nyhamn, Gotland.

Diagnosis.—As for the genus.

Description.—The only traces of lobation are those mentioned in the generic diagnosis; as no male specimens have been found, it is not known whether the species has a syllobial groove like almost all craspedobolbinine genera. Velum wide and tubulous beginning in both valves at a process very similar to or even identical with the acroidal processes widening ventrally and tapering again towards a similar process posteriorly. Crumina suggestive of a silk cocoon; less than one third of it is situated behind a line drawn through

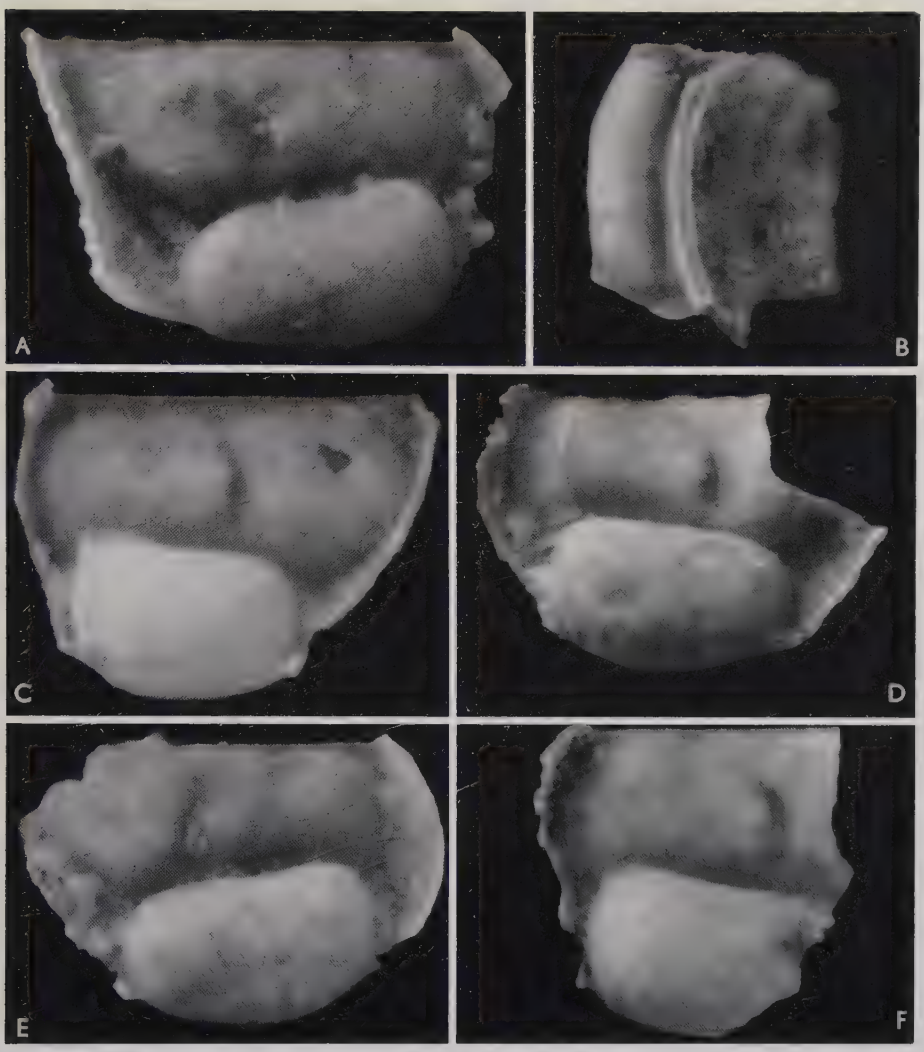


Fig. 88. *Barymetopon infantile* n.sp. Female valves from the Lower Visby Beds at Nyhamn. × 50. A. No. G 407 (holotype). B. No. G 408, ventral view of the crumina, anterior end up. C. No. G 409. D. No. G 417. E. No. 418. F. No. G 419.

the sulcus. The velum encroaches onto the end of the crumina, and there is a great distance between its ends and the long dolonoid scar; the scar is possibly constructed in the same way as in *Clintiella*. Valve surface smooth, crumina finely striate ventrally.

The small thinly reniform sulcus is situated in such a position that the larger part of the valve surface lies in front of it; the postadductorial part of the valve tapers strongly towards the posterior hinge corner.

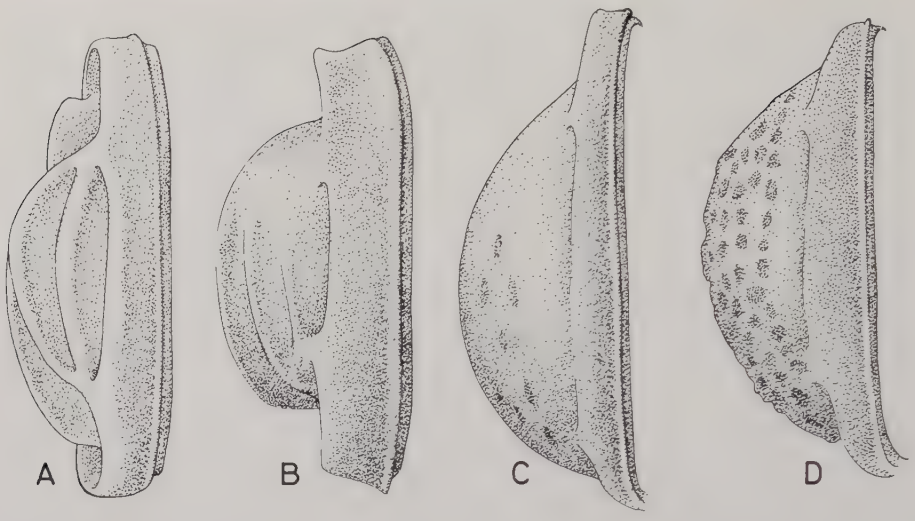


Fig. 89. Ventral morphology of the crumina in European Silurian *Treposellinae*. A. *Strepula* Jones & Holl, based on *S. irregularis* (Jones & Holl). B. *Garniella* n.g., based on *G. lineolata* n.sp. C. *Bolbiprimitia* (ventral morphology of the American type species unknown), based on *B. inaequalis* (Jones). D. *Retisacculus* n.g., based on *R. semicolonatus* n.sp. A ×40, B ×75, C ×40, D ×60.

Dimensions.—Hinge length–sulcal height of female valves: 1100 μ – 850 μ, 1065 μ – 830 μ.

Remarks.—The eight specimens found are all adult females.

Occurrence.—Lower Visby Beds: Nyhamn.

Subfamily *Treposellinae* Henningsmoen 1954

Fig. 89.

Type Genus.—*Treposella* Ulrich & Bassler 1908

Genera.—*Strepula* Jones & Holl 1886
Garniella n.g.
Bolbiprimitia Kay 1940 *Retisacculus* n.g.
Hibbardia Kesling 1953
Kozlowskiella Přibyl 1953
Treposella Ulrich & Bassler 1908
Phlyctiscapha Kesling 1953

Diagnosis.—*Beyrichiidae* tending to incorporate, or incorporating, a large part of the syllobium with an originally anteroventral crumina, the dolonoid closing mechanism of which has largely become obsolete.

Remarks.—A survey of common lobal and ornamental structures shows that all genera except *Phlyctiscapha* have traces of at least a preadductorial

node in front of a more or less reduced adductorial sulcus; only one genus, *Strepula*, has a fully developed beyrichiid lobation, but both sulci are also present in *Treposella*. It is questionable whether a syllobial groove exists; in some *Garniella* species there is a groove breaking the reticulation in the corresponding region, and in *Treposella* there is a shallow depression similar to the syllobial groove. Except in *Phlyctiscapha* the carapace is reticulate; the reticulation is sometimes very similar to that in the craspedobolbinine genus *Clintiella*. Cristae occur, both on the lobes and on the crumina, in some genera.

There is no certain calcarine tubercle observed in this subfamily; possibly the cruminal crista in *Treposella stellata* ends in a similar structure (Kesling 1957b, Pl. VI, figs. 5–6).

Tubulosity in the marginal structures (which are very incompletely known) exists, at least, in *Treposella*, *Hibbardia*, *Strepula*, and *Garniella*; the velum is tubulous in *Treposella stellata*, and, possibly, in some species of *Strepula* and *Garniella*; the typical treposelline velum is, however, narrow.

Really typical dolonoid scars occur only in the last two genera to be described, *Treposella* and *Hibbardia*, which are from several points of view more primitive or conservative than the Silurian forms known. In *Treposella* the granulation still covers the reticulation meshes, and in its type species the well delimited crumina is striate.

The *Treposellinae* had probably close ancestors in common with the craspedobolbinines with a long crumina and a tendency to punctation and reticulation. The problem of "*Bolbiprimitia*" *limbata* and "*B.*" *teresaccula* has already been dealt with above (p. 190).

Genus *Strepula* Jones & Holl 1886

Figs. 89A and 90.

Type Species.—*Strepula concentrica* Jones & Holl 1886, designated by Bassler & Kellett 1934, p. 476.

Species.—Only the type species (as pointed out above, p. 25, *S. irregularis* is conspecific with the type species).

Diagnosis.—*Treposellinae* with anterior lobe, preadductorial knob, and syllobium, and a crumina which is cristate like the lobes.

Remarks.—The wanderings of *Strepula* from having been associated with *Kirkbya* by Jones & Holl, through the *Beyrichiidae*, *Kirkbyidae*, *Piretellidae* (*Bassleratiinae*) and its association with the most different forms can be followed in the index papers (Bassler & Kellett 1934; Howe 1955).

The genus unites the trends towards the typical treposellines with a lobation and cristation found very far down in the beyrichiid system.

Occurrence.—Silurian of England.

Fig. 90. *Strepula* Jones & Holl 1886. Drawing based on *Strepula concentrica* Jones & Holl 1886. ×45. A. Female. B. Male.

Strepula concentrica Jones & Holl 1886

Figs. 2E–F, 89A, 90, and 92A–B.

1886 *Strepula concentrica* sp. nov.—Jones & Holl 1886b, p. 404; Pl. XIII: 4 (*non 1*).
1886 *Strepula irregularis* sp. nov.—Jones & Holl 1886b, p. 404; Pl. XIII: 7–8.

Lectotype.—Designated herein, p. 25 (cf. l.c. for comments on type occurrence).

Diagnosis.—As for the genus.

Description.—Anterior lobe with one crista from the cusp, in the male bending backwards, ending with a bend round the posteroventral part of the syllobium. In the female it is interrupted by the crumina, and its posterior part bends down and touches a new crista on the crumina. The zygal crista can be followed in the male from the upper part of the preadductorial knob over the zygal arch onto a syllobial cusp; however it branches into a fine crista on the syllobium behind the sulcus. In the female the zygal crista is interrupted by the crumina. There is another small crista along the cuspidal plica of the syllobium. Reticulation absent along the velum and in the sulci.

Velar structure flangelike; radial structures seen in transmitted light may represent a rudimentary tubulosity. The crumina still forms a globular swelling below the preadductorial node, but parts of the velum and the carapace wall behind it have been incorporated.

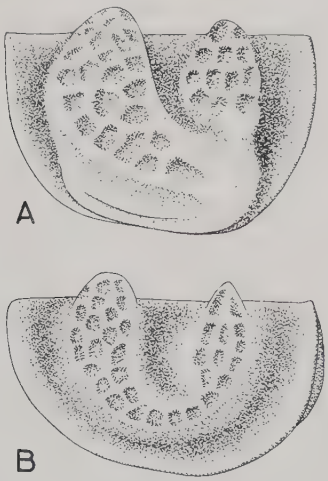


Fig. 91. *Garniella* n.g. Drawing based on *Garniella lineolata* n.sp. ×60. A. Female. B. Male.

Dimensions.—Hinge length of a female specimen from Harley Hill road cutting, Shropshire, 1180 μ, sulcal height 865 μ.

Occurrence.—Silurian of England.

Genus *Garniella* n.g.

Fig. 91.

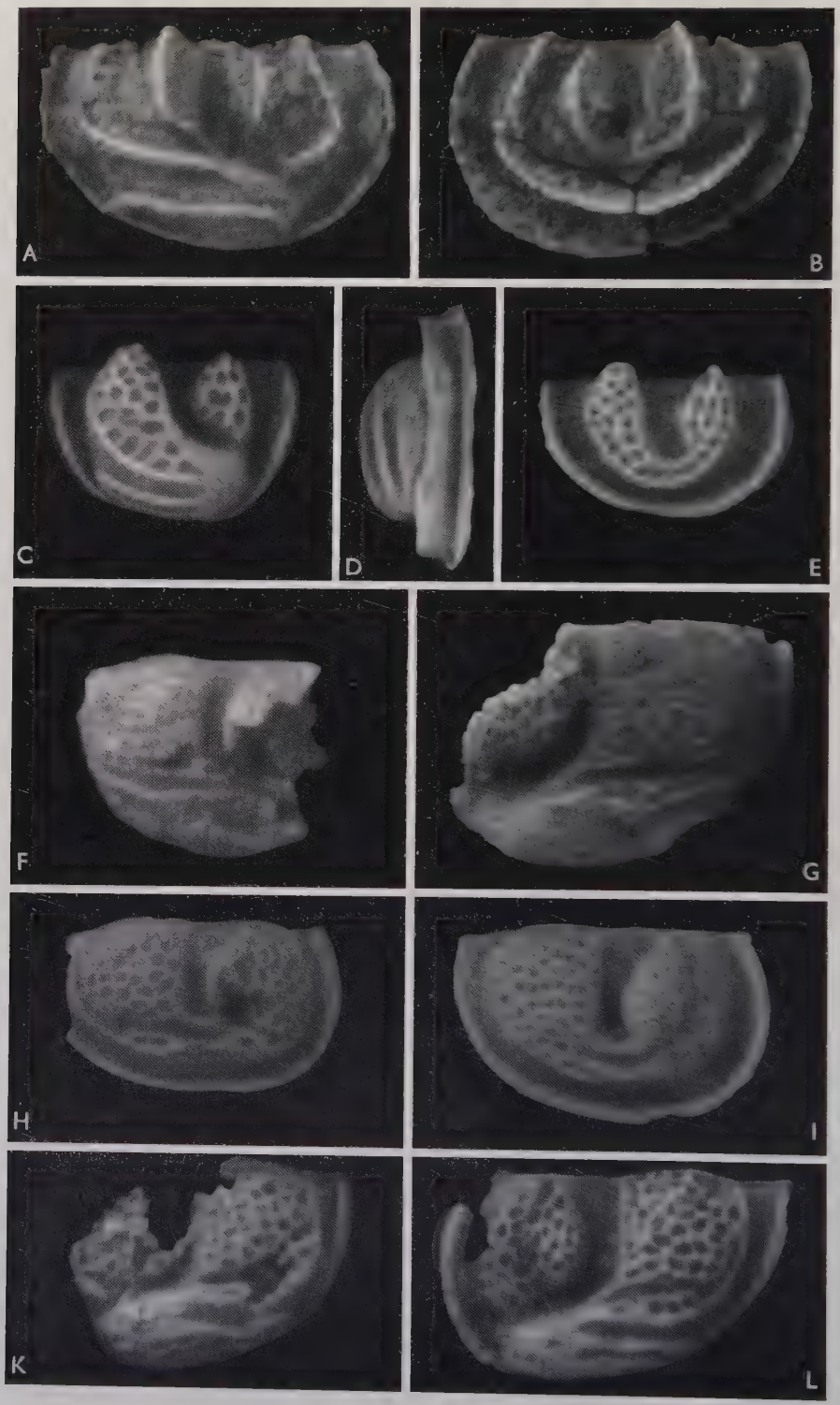
Derivation of the Name.—Feminine diminutive of a Latin adjective *Garnius*, associated with the parish of Östergarn.

Type Species.—*Garniella lineolata* n.sp.

Species.—*Garniella lineolata* n.sp.
Garniella jugata n.sp.
Garniella uniseriata n.sp.
Garniella biseriata n.sp.
Garniella strepuloides n.sp.

Diagnosis.—*Treposellinae* with reticulate lobes and cristae only on the crumina.

General Description.—The lobes are coarsely reticulate; the adductorial sulcus and the velum are smooth. Syllobium generally broad, with a low dorsal ridge (exception: *G. lineolata*). The preadductorial node and the anterior lobe form a complex in which the preadductorial node can be more or less clearly distinguished (exception: *G. lineolata*). Crumina fused with the syllobium, provided with cristal ridges which may be split up by the reticulation into series of meshes (there is a tendency to such splitting and assimilation of the cristae with the reticulation in *Strepula*, too). The velum forms two bridges fused with the crumina.


A
B
C
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L

Garniella lineolata n.sp.

Figs. 89B, 91 and 92C–E.

Derivation of the Name.—Latin *lineolatus*, provided with small lines, referring to the cristae on the crumina.

Holotype.—A right female valve, No. G421 (Fig. 92C–D).

Type Stratum and Type Locality.—Hemse Beds at Hammarudden, Gotland.

Diagnosis.—*Garniella* sp. with simple cristae on the crumina and with pointed lobes.

Description.—Syllobium comparatively narrow, with its stout, pointed dorsal end protruding over the hingeline; anterior lobal complex equally pointed; anterior lobe probably totally fused with the preadductorial node. The syllobium is four meshes wide, the anterior complex three or four. In the tecnomorph there is a single zygal row of meshes below the sulcus. There are two simple cristae lateroventrally on the crumina, below the reticulate field of the syllobium.

Dimensions.—Hinge length of a female specimen from Hammarudden 720 μ, sulcal height 495 μ. Three female valves from Tänglings: 800 μ – 480 μ, 770 μ – 510 μ, 730 μ – 480 μ.

Remarks.—The narrow pointed syllobium, the undifferentiated anterior lobal complex, and the simple cristae on the crumina distinguish this species from all other species in the genus. At any rate the lobal morphology is certainly a function of the extremely small size.

Occurrence.—Hemse Beds: Hammarudden (very rare), Tänglings (rare).

Garniella jugata n.sp.

Figs. 92I–L, *G.* cf. *jugata* Figs. 92F–H.

Derivation of the Name.—Latin *iugatus*, provided with a yoke, referring to the distinct zygal arch.

Holotype.—A left, somewhat fragmentary female valve, No. G429 (Fig. 92L).

Type Stratum and Type Locality.—Slite Beds at Stora Banne, Gotland.

Diagnosis.—*Garniella* sp. with zygal arch set off from the nearest row of meshes by an unornamented groove.

Description.—Anterior lobe set off from the preadductorial node by an

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Fig. 92 (opposite page). A–B. *Strepula concentrica* Jones & Holl 1886, road section in Wenlock Shale at Harley Hill, Shropshire. ×40. A. Female valve, No. EW 4. B. Male valve, No. EW 5. C–E. *Garniella lineolata* n.sp., Hemse Beds, Hammarudden. ×50. C–D. Female valve, No. G 421 (holotype). E. Tecnomorph, No. G 423. F–H. *Garniella* cf. *jugata* n.sp., Tofta Beds, Bingers. ×40. F. Right female valve, No. G 424. G. Left female valve, No. G 425. H. Tecnomorph, No. G 426. I–L. *Garniella jugata* n.sp., Slite Beds, Stora Banne. ×40. I. Tecnomorph, No. G 427. K. Fragmentary left female valve, No. G 428. L. Female valve, No. G 429 (holotype).

ornamented sulcoid depression, zygal region in the male as stated in the diagnosis, syllobium broad. Zygal ridge broken by the crumina; the row of meshes below the original zygal arch encroaches onto the crumina; there are two more ridges below it, partly connected by a reticulation.

Dimensions.—Hinge length of the holotype ca. 1200 μ, sulcal height 720 μ.

Remarks.—The morphology of the zygal region distinguishes this species from all other *Garniella* species; the female has the single row of meshes on the crumina in common with *G. uniseriata* but is easily distinguished from this species by the more marked preadductorial node.

Occurrence.—Slite Beds: Stora Banne (rare).

Garniella cf. *jugata* is also found in the Tofta Beds at Bingers; it differs slightly from the younger material by the more pronounced continuation of the subzygal (syllobial?) groove across the syllobium and a less marked depression in front of the preadductorial node (cf. Figs. 92 F–H).

Garniella uniseriata n.sp.

Figs. 93A–B.

Derivation of the Name.—Latin *uniseriatus*, provided with one row (of meshes).

Holotype.—A right female valve, No. G430 (Fig. 93A).

Type Stratum and Type Locality.—Klinteberg Beds at Hunninge, Gotland.

Diagnosis.—*Garniella* sp. without a free zygal arch in the male; there is one row of meshes encroaching onto the crumina.

Description.—The anterior lobe and the preadductorial node are fused without any considerable sulcal depression. Syllobium broad with a dorsal ridge gently curved over the level of the hingeline, connected in the tecnomorphs with the syllobium by an area of effaced ornamentation; there is, however, no distinct groove in this place extending onto the syllobium. There are two more indistinct cristae below the row of meshes on the crumina.

Dimensions.—Hinge length of the holotype 1310 μ; sulcal height 930 μ.

Remarks.—This species is very similar to *G. jugata* but differs from it by the more complete fusion in the preadductorial lobe complex and by the absence of a marked groove below the zygal arch.

Occurrence.—Klinteberg Beds: Klinte, Hunninge (rare).

Garniella biseriata n.sp.

Figs. 93C–D.

Derivation of the Name.—Latin *biseriatus*, provided with two rows (of meshes in the reticulation of the crumina).

Holotype.—A right female valve, No. G432 (Fig. 93C).

Type Stratum and Type Locality.—Slite Beds at Norrbys, Gotland.

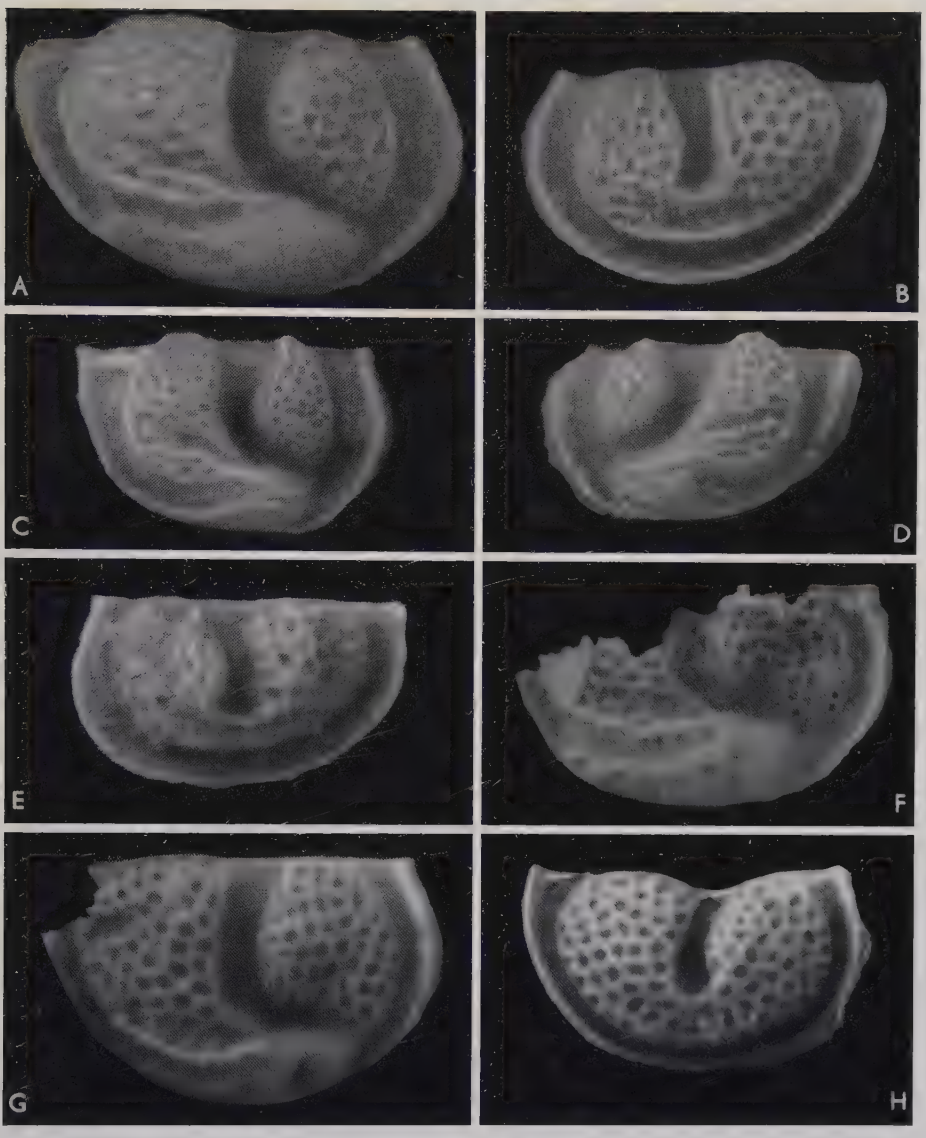

Fig. 93. A–B. *Garniella uniseriata* n.sp., Klinteberg Beds, Hunninge. ×40. A. Female valve, No. G 430 (holotype). B. Tecnomorph, No. G 431. C–D. *Garniella biseriata* n.sp., Slite Beds. ×40. C. Female valve from Norrbys, No. G 432 (holotype). D. Female valve from Follingbo III, No. G 433. E. *Garniella* sp., Slite Beds, Follingbo I, No. G 434. ×40. F–H. *Garniella strepuloides* n.sp., Hemse Beds, Tänglings. ×40. F. Left female valve, No. G 435. G. Female valve, No. G 436. H. Tecnomorph, No. G 437.

DIAGNOSIS.—*Garniella* sp. with two rows of meshes in the reticulation posterodorsally on the crumina.

DESCRIPTION.—Anterior lobe and preadductorial node completely fused. Syllobium relatively narrow; its rounded dorsal end protrudes considerably

over the hingeline. The cristal ridge corresponding to the subzygal ridge in *G. jugata* divides posteriorly into two rows of meshes separated from the non-cruminal syllobial reticulation by a groove; there is also a reticulation ventrally on the crumina between the two ventral cristae.

Dimensions.—Hinge length–sulcal height of a female valve from Norrbys 1000 μ – 680 μ; from Follingbo III 980 μ – 630 μ.

Remarks.—The two rows of meshes on the crumina are sufficient to distinguish this species from all other *Garniella* species. Its lobal features show some similarity to *G. lineolata*. Great efforts have been made to find the tecnomorphs of this species, but in vain. Tecnomorphs of *Garniella* have been found both at Follingbo III and Follingbo I, but they belong to a species with a wide velum with a differentiation of the anterior lobal complex similar to that in *G. jugata* but lacking the distinct differentiation of a zygal and a subzygal ridge (Fig. 93 E). The velum of this species shows radial structures which doubtless prove the obsoletion of the tubulosity in the Silurian group of treposellines.

Occurrence.—Slite Beds: Norrbys, Follingbo III (very rare).

Garniella strepuloides n.sp.

Figs. 93 F–H.

Derivation of the Name.—From the generic name *Strepula* (*fide* Jones & Holl 1886b a diminutive of a "Latin" word for stirrup), and the latinized Greek suffix *-oides*, similar to.

Holotype.—A right female valve, No. G436 (Fig. 93 G).

Type Stratum and Type Locality.—Hemse Beds at Tänglings.

Diagnosis.—*Garniella* sp. with anterior lobal complex only inconsiderably narrower than the syllobium. Reticulation preserved between all cristae on the syllobium.

Description.—The anterior lobe is very broad and completely fused with the preadductorial node. In the male there is a very broad connection below the sulcus between the two main lobal areas. The female shows only a comparatively slight differentiation of cristae on the crumina, and the reticulation continues onto the cristal ridges, tending to split them up, as is the case in *Strepula*. Posteroventral part of the crumina reticulate.

Dimensions.—Hinge length of the best preserved female valve from Tänglings, the holotype, ca. 1310 μ, height over sulcus 905 μ.

Remarks.—The broad anterior lobal complex and the intercristal ornamentation on the crumina distinguish this species from all other *Garniella* species.

Occurrence.—Hemse Beds: Tänglings (very rare).

Genus *Retisacculus* n.g.

Figs. 89 D and 94.

Derivation of the Name.—Latin *rete*, net, and *sacculus*, small sack.

Type Species.—*Retisacculus commatatus* n.sp.

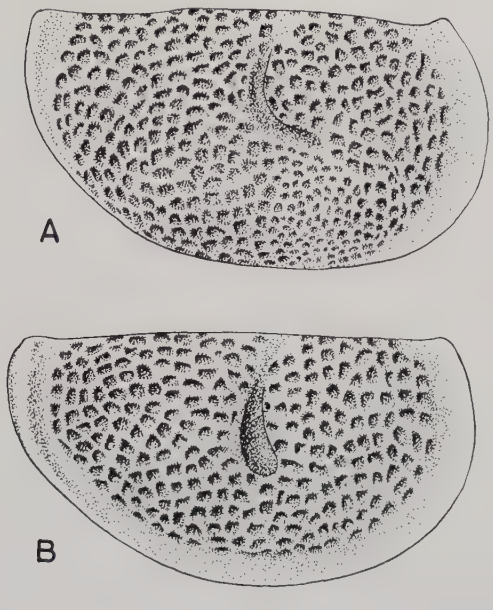

Fig. 94. *Retisacculus* n.g. Drawing based on specimens of *Retisacculus commatatus* n.sp. ×45. A. Female. B. Male.

Species.—*Retisacculus commatatus* n.sp.
Retisacculus semicolonatus n.sp.

Diagnosis.—*Treposellinae* with reticulation over the whole carapace, including the crumina. Smooth, narrow velar flange. Prenodal sulcus completely obsolete, adductorial sulcus constricted near the hinge or at its mid-length.

General Description.—In both species the sulcus curves around the preadductorial node which is otherwise completely fused with the anterior lobe. There is a broad reticulate field between the lower end of the sulcus and the velum, connecting the anterior lobal complex and the syllobium; the velar edge is somewhat thickened. The crumina is completely reticulate and is not set off from the syllobium; there are two widely separated bridges at the junctions of the precruminal and postcruminal parts of the velum and the ridge connecting these velar portions along the ventral side of the crumina. Vertical marginal structure fine, ridge-like on the right valve, somewhat more flange-like on the left valve which also has the covering, narrowly flange-like structure. There is no distinct tubulosity in the marginal structures.

Remarks.—It is problematic whether it is logical to place this genus between the genera *Garniella* and *Bolbiprimitia*; the lobation, including the incorporation of the crumina with the syllobium, is more advanced, but the ventral morphology of the crumina shows more pronounced "treposelline bridges". The interior of the crumina has not yet been investigated.

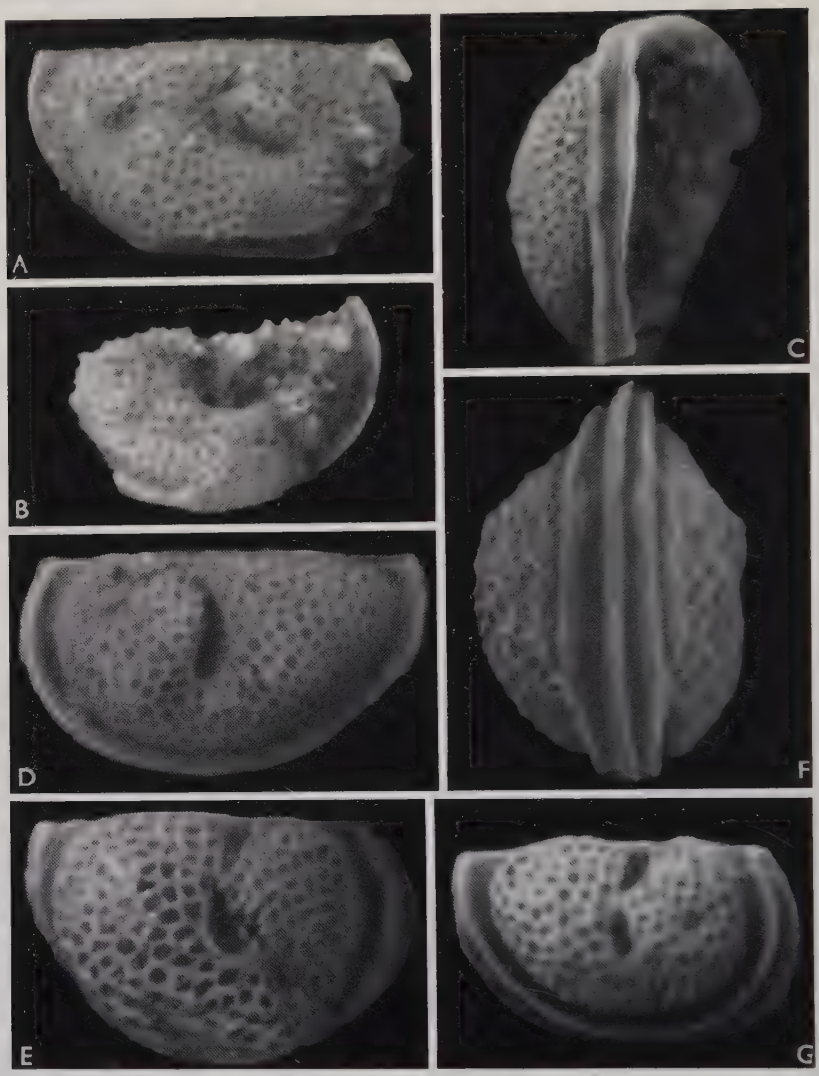

Fig. 95. A–D. *Retisacculus commatatus* n.sp., Eke Beds, Lau Backar. ×40. A. Female valve, No. G 438 (holotype). B. Right female valve, No. G 439. C. Female valve in ventral view, anterior end up, No. G 443. D. Male valve, No. G 440. E–G. *Retisacculus semicolonatus* n.sp., Hamra Beds, Sles. ×50. E–F. Female carapace in lateral and ventral (anterior end up) views, No. G 441 (holotype). G. Tecnomorphic carapace, No. G 442.

Retisacculus commatatus n.sp.

Figs. 95A–D.

Derivation of the Name.—Latin *commatatus*, provided with a comma, referring to the shape of the adductorial sulcus.

Holotype.—A fragmentary right female valve, No. G438 (Fig. 95A).

Type Stratum and Type Locality.—Eke Beds at Lau Backar, Gotland.

DIAGNOSIS.—*Retisacculus* sp. with a sulcus shaped like an inverted comma, in the female somewhat distorted by the crumina. Reticulation slightly finer anteriorly on the crumina.

DESCRIPTION.—See diagnoses and general generic description.

DIMENSIONS.—Hinge length of the holotype 1280 μ, sulcal height (measured from the hingeline to the free margin) 785 μ.

REMARKS.—This species differs from *R. semicolonatus* by its undivided sulcus.

OCCURRENCE.—Eke Beds: Lau backar (extremely rare).

In the Hamra Beds some tecnomorphs referred to as *R.* cf. *commatatus* have been found: Hoburgen Ia, Hoburgen IIa, Hoburgen IIb. Only one tecnomorphic specimen has been found in the Sundre Beds, at Hoburgen Ib.

Retisacculus semicolonatus n.sp.

Figs. 95E–G.

DERIVATION OF THE NAME.—Latin *semicolonatus*, provided with a semicolon, referring to the shape of the sulcus.

HOLOTYPE.—A female carapace, No. G441 (Fig. 95E–F).

TYPE STRATUM AND TYPE LOCALITY.—Hamra Beds at Sles, Gotland.

DIAGNOSIS.—*Retisacculus* sp. with sulcus constricted at mid-length by a direct connection between the preadductorial node and the syllobium; reticulation without any differentiation on the crumina.

DESCRIPTION.—See diagnoses and general generic description.

DIMENSIONS.—Hinge length–sulcal height of a female valve from Sles, 811 μ–630 μ; a female valve from Lunde 880 μ–585 μ.

REMARKS.—This species differs from *R. commatatus* and all other known *Beyrichiidae* by the bipartition of the sulcus.

OCCURRENCE.—Hamra Beds: Sles, Lunde (rare).

Genus *Bolbiprimitia* KAY 1940

Fig. 89C.

TYPE SPECIES.—*Halliella fissurella* ULRICH & BASSLER 1923

SPECIES.—*Halliella fissurella* ULRICH & BASSLER 1923
Primitia inaequalis JONES 1888
Bolbiprimitia falculata n.sp.

DIAGNOSIS.—*Treposellinae* with a flattened, reticulate anterior lobal complex, a flattened, reticulate syllobium, and with a broad connection between these elements below the adductorial sulcus. The preadductorial node forms a small bulge in the anterior margin of the sulcus. Crumina smooth, without cristae.

REMARKS.—The only information obtainable as to the ventral morphology of the crumina in the type species, *Bolbiprimitia fissurella*, is a reconstructive drawing by KESLING (1957b, Pl. II, fig. 6). In comparison with figures given

here (Figs. 89C and 96C–D) the reconstruction mentioned shows essential differences as to the "treposelline bridges", but this may depend on the fact that dolonoid scars and associated features were unknown at the time of reconstruction. As an investigation of the cruminal morphology of the type species is essential for a revision of the genus, the Silurian species from Gotland mentioned (as well as *Halliella* aff. *fissurella* described from the Devonian of the U.S.S.R. by POLENOVA 1955) are provisionally—following MARTINSSON 1956, pp. 23–25—referred to *Bolbiprimitia*.

Bolbiprimitia inaequalis (JONES 1888)

Figs. 89C and 96A–F.

REMARKS.—This species has recently been treated taxionomically by MARTINSSON (1956, pp. 24–25). Some essential new observations on its morphology should be added.

In an earlier generic diagnosis (MARTINSSON 1956, p. 23) attention was drawn to the fact that the velum—in contrast to the conditions in *Beyrichia* s.l. —is developed right along the free margin. As now known this is not quite correctly expressed. There are traces of fine "treposelline bridges" anteriorly and posteriorly at the ventral base of the crumina (Figs. 96C–D) and, if there are any closer relationships with *Clintiella* (*via* forms with a crumina similar to that in *B. limbata* and *B. teresaccula* SWARTZ & WHITMORE 1956), the real homologue of the velar edge is to be found in the furrow outside that ridge which morphologically forms a perfect connection between the pre- and postcruminal velar portions.

Thin sections have been made in order to prove this, but the results are not completely conclusive. In *Clintiella hyrsiniana* the part of the cruminal wall which in other genera is clearly derived from the flap, is clearly isolated from that part of the carapace wall which forms the velum-like ridge. The ridge is a fold with a "bisecting line" as found in different fold-like structures in the ostracode carapace. These conditions prove the homology of the furrow with the dolonoid scar in the other genera; it is possible that the formation of a dolonoid pouch in the other genera has been reduced to only a long, fold-like groove in *Clintiella*.

In *Bolbiprimitia inaequalis* the ridge on the two cruminae investigated (female specimens are very rare) is developed in the same way as in *Clintiella*, but the state of preservation does not make it possible to establish whether the furrow

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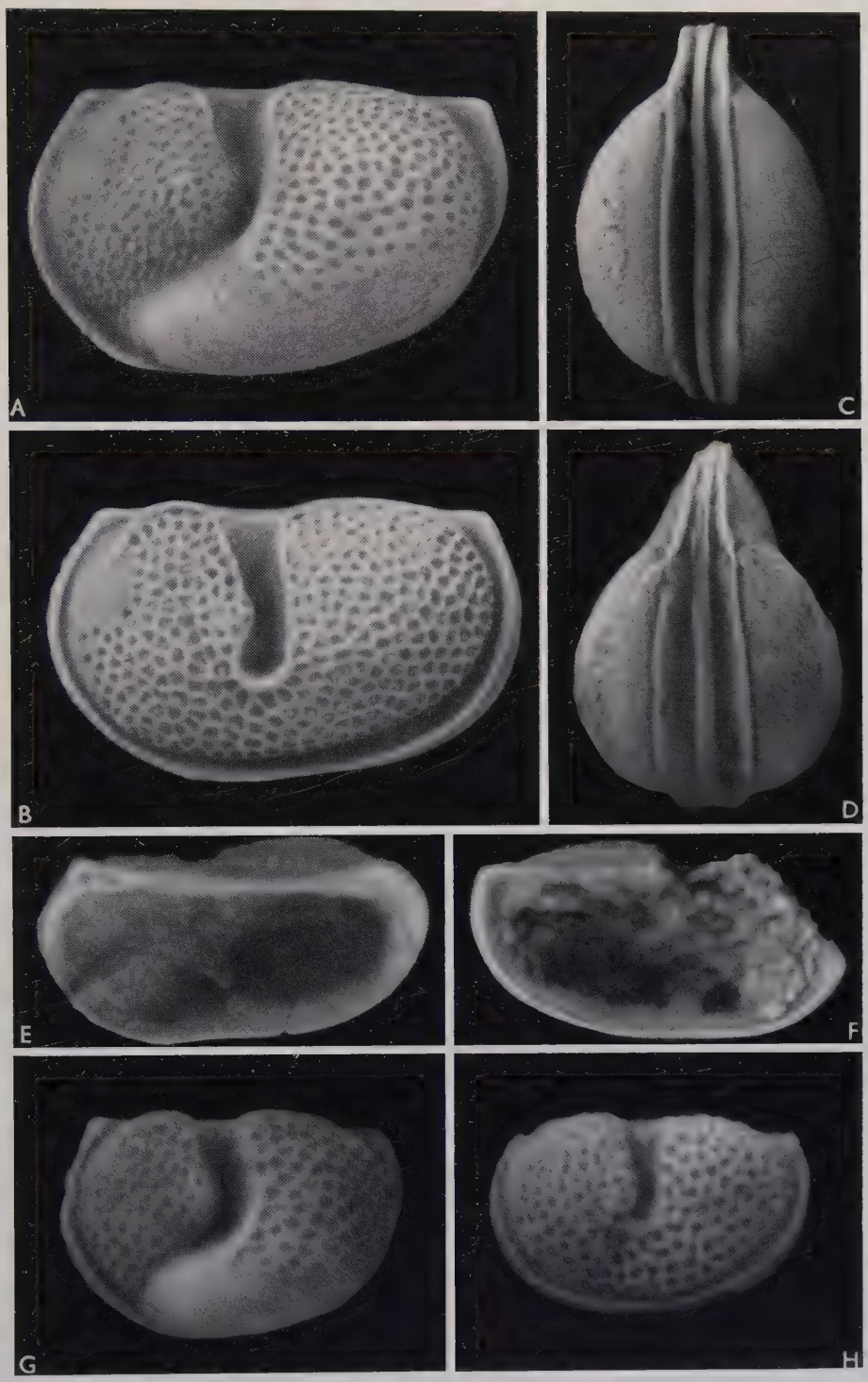
Fig. 96. A–F. *Bolbiprimitia inaequalis* (JONES 1888). A. Female carapace, No. G 444. ×40. B. Male carapace, No. G 446. ×40. C–D. Female carapaces in ventral view, Nos. G 445 and G 447. ×30. E–F. Female valves, interior view, showing the strut across the region of the cruminal opening, Nos. G 448 and G 449. ×30. G–H. *Bolbiprimitia falculata* n.sp., Slite Beds. ×40. G. Female valve from Längars, No. G 450 (holotype). H. Tecnomorph from Gane, No. G 451.


A
C
B
D
E
F
G
H

outside it penetrates the cruminal wall completely, as in *Clintiella*, or is a simple inward fold. This part of the investigation is being continued in connection with a general investigation of the cruminae and their contents, based on sections.

In spite of the wide opening of the crumina a specimen shows that the numerous larvae were still retained in the cruminae after death; this specimen may, however, have been embedded standing on the ventral side. At least nine larval specimens were observed during the grinding of half of the length of the cruminae. They were of the same size as far as can be judged by subjective observation.

The preparation of the cruminae by scooping out the marl substance from the inside of the carapace has proved the existence of a strut across the crumina from the zygal region to the marginal region (Figs. 96E–F, cf. KESLING 1957a). Unfortunately the cruminae and other small spaces, such as folds and the space between fossil fragments, are always centres of rechrystallization which makes it difficult to make satisfactory preparations of the interior of the crumina.

Bolbiprimitia falculata n.sp.

Figs. 96G–H.

DERIVATION OF THE NAME.—Latin *falculatus*, provided with a small knife, referring to the outline of the sulcus in the female.

HOLOTYPE.—A left female valve, No. G450 (Fig. 96G).

TYPE STRATUM AND TYPE LOCALITY.—Slite Beds at Längars, Gotland.

DIAGNOSIS.—Small *Bolbiprimitia* sp. with about eight meshes in the reticulation of the syllobium between the sulcus and the posterior part of the velar flange.

DESCRIPTION.—The broad anterior lobal complex is smooth in an area near the anterior hinge corner and has a rounded dorsal ridge which protrudes slightly over the hingeline. The small preadductorial node is completely fused with the anterior lobe but forms a bulge in the adductorial sulcus very near its lower end. The syllobium is entirely reticulate and forms a dorsal ridge like that of the anterior lobal complex. The presulcal and the ventral parts of the crumina are entirely smooth.

DIMENSIONS.—Hinge length of the holotype 1110 μ, sulcal height 825 μ.

REMARKS.—This species differs from *B. inaequalis* by its considerably smaller size (Figs. 96A–B and G–H are on the same scale), the site of the preadductorial node immediately above the lower end of the sulcus, and by the number of meshes in the reticulation (the last-mentioned qualities could be functions of the small size). There are about 8 meshes horizontally on the syllobium against about 12–13 in *B. inaequalis*; vertically across the male syllobium the numbers are about 11 and about 19–20, respectively.

OCCURRENCE.—Slite Beds: Längars (the only female specimen and a few tecnomorphs), Slite I (a few tecnomorphs), Gane (one tecnomorph).

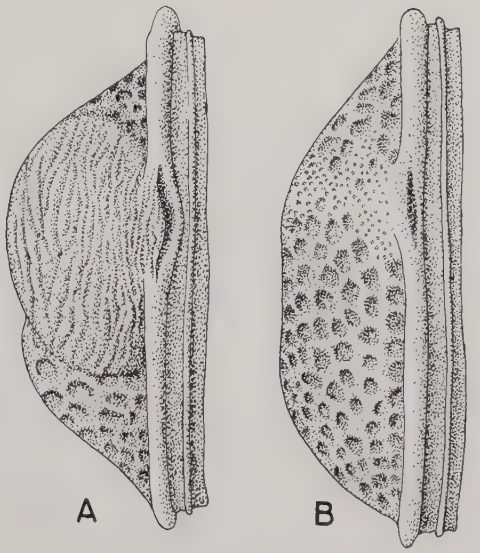


Fig. 97. Ventral morphology of the crumina in North American Devonian *Treposellinae*. ×40. A. *Treposella* Ulrich & Bassler 1908, reconstruction based on photographs of a specimen of *T. lyoni* published by Kesling & Rogers 1957, Pl. 127, figs. 1–3. B. *Hibbardia* Kesling 1953, drawing based on photographs published by Kesling & Rogers 1957, Pl. 127, Figs. 22–26.

Genus *Hibbardia* Kesling 1953

Fig. 97B.

Remarks.—This genus has been excellently figured in photographs and drawings by Kesling (1953, 1954, 1957a, and 1957b, cf. Kesling & Rogers 1957), and there is no difficulty in making a clear picture of the external traces of the anteroventral origin of the cruminal development.

Like *Treposella* (cf. below), *Hibbardia* has a small scar anteroventrally, situated within the present velar flange. The velar edge passes into two bridges over to the carapace wall which is in this species much more finely reticulate in the anteroventral part of the female than in other parts of the carapace. As discovered by Kesling (1957a) this species has an internal strut in the crumina like that now found in *Bolbiprimitia*. The dolonoid scar is marked in the reconstruction given by Kesling (1957 b, Pl. VII, fig. 3); dolonoid scars should be added to the otherwise excellent reconstructions of *Apatobolbina*, *Bolbineossia* ("*Chilobolbina*" sp.), *Bolbibollia*, *Craspedobolbina armata*, and *Treposella lyoni* in the same paper. *Treposella stellata* and *Bolbiprimitia fissurella* require further investigations in this respect.

Genus *Treposella* Ulrich & Bassler 1908

Fig. 97A.

Remarks.—This geologically late treposelline has an anterior scar of the same kind as in *Hibbardia* and presents primitive features in the lobation and in the

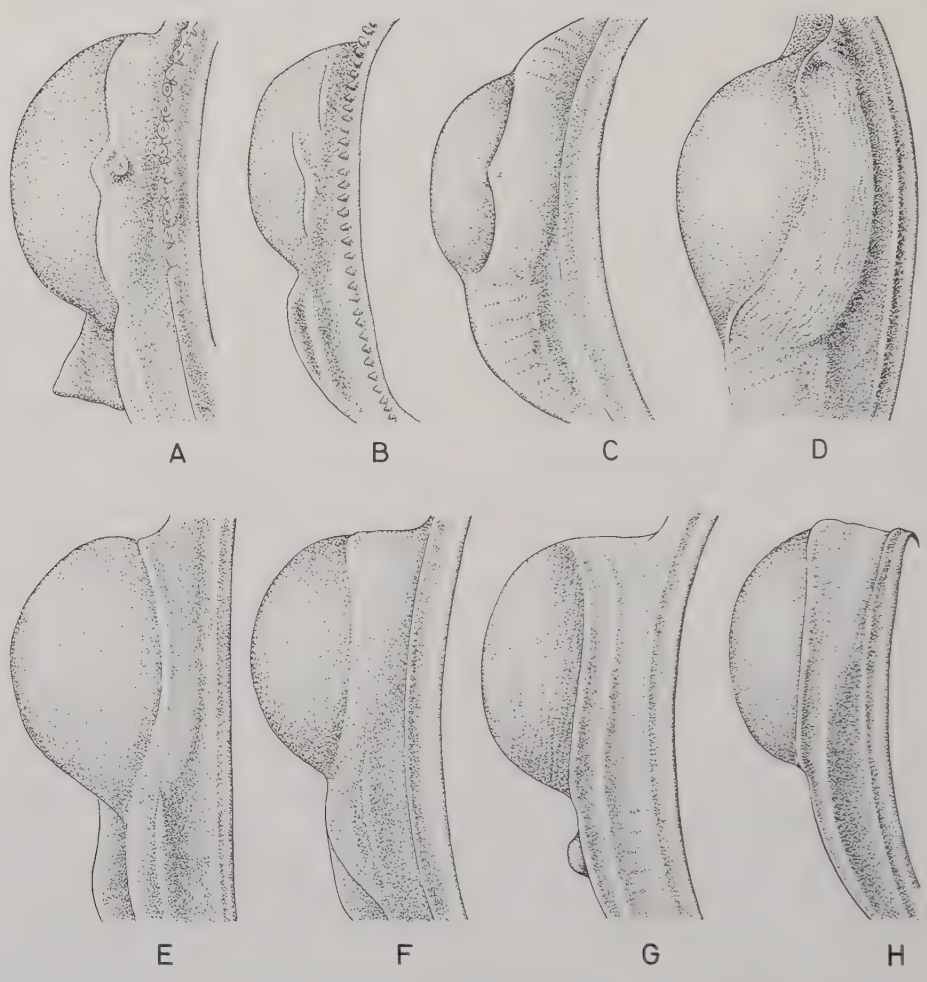


Fig. 98. Morphology of the ventral side of the crumina in the subfamily *Amphitoxotidinae*. A–B. *Sleia* n.g., drawings based on *Sleia equestris* n.sp. (A) and *Sleia troglodytophila* n.sp. (B). C. Undescribed Wenlockian genus from Britain (cf. Fig. 100 D). D. Undescribed Wenlockian genus from Britain (cf. Fig. 100 E). E. *Amphitoxotis* n.g. based on *Amphitoxotis curvata* n.sp. F. *Cryptolopholobus* n.g., based on *Cryptolopholobus semilaqueatus* n.sp. G. *Lophoctenella* n.g., based on *Lophoctenella angustilaqueata* n.sp. H. Undescribed Wenlockian genus from Britain (probably including *Beyrichia Kloedeni* var. *granulata* JONES, as illustrated by JONES & HOLL 1886 a, Pl. XII, fig. 3). A ×40, B ×40, C ×40, D ×40, E ×60, F ×50, G ×40, H ×40.

cruminal development. The crumina is well delimited both lobally and ornamentally, but there is no doubt that it represents an early stage in the trend towards an incorporation of the crumina with the syllobium. The striation of the crumina continues down into the dolonoid scar, and the small ridge delimiting this scar is never so high that it is suggestive of being a part of the velar flange as in *Hibbardia*. It is always dangerous to base a judgement solely on figures, however excellent these may be (KESLING & ROGERS 1957, Pl. 127,

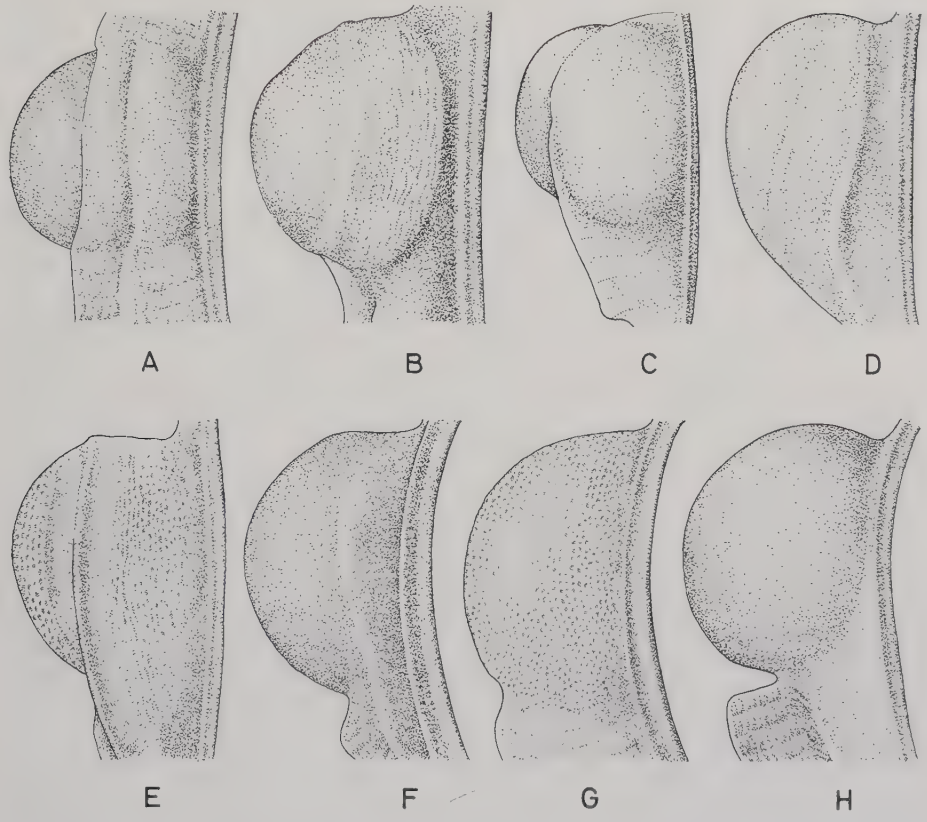


Fig. 99. Morphology of the ventral side of the crumina in the subfamily *Amphitoxotidinae* (continued). A. *Hoburgiella* n.g., drawing based on *Hoburgiella tenerrima* n.sp. B. *Vinculoveliger* n.g., based on *Vinculoveliger catenulatus* n.sp. C. *Hemsiella* n.g., based on *Hemsiella pulchricruminata* n.sp. D. *Lauella* n.g., based on *Lauella* sp. from Hammarudden. E. *Hemsiella loensis* n.sp. F. *Juviella* n.g., based on *Juviella juvensis* n.sp. G. *Hammariella* n.g., based on *Hammariella pulchrivelata* n.sp. H. *Atterdagia* n.g., based on *Atterdagia paucilobata* n.sp. A ×70, B ×40, C ×70, D ×50, E ×50, F ×50, G ×60, H 40.

fig. 3), but it seems that the morphology of the dolonoid scar is more craspedobolbinine-like than in any other treposelline.

Treposella stellata differs from *T. lyoni* in several major features, as the wide, tubulous velum and the smooth, cristate crumina. The dolonoid scar in this species cannot be reconstructed from the photographs published (cf. KESLING & ROGERS 1957, Pl. 127, fig. 7).

In several genera, then, it is clearly shown that primitive features in the development of the treposelline crumina are associated with the anteroventral part of the carapace. These genera are *Strepula*, *Retisacculus* (finer anteroventral reticulation in *R. commatatus*), *Treposella*, and *Hibbardia*. The smooth part of the crumina in *Garniella* and *Bolbiprimitia* marks the site of the primordial

crumina. *Kozlowskiella* is more advanced in the reduction of the traces of the dolonoid development, but tendencies towards the formation of "treposelline bridges" possibly exist.

Subfamily *Amphitoxotidinae* n. subf.

Figs. 98–100.

TYPE GENUS.— *Amphitoxotis* n.g.

GENERA.—*Sleia* n.g.
Hemsiella n.g.
Amphitoxotis n.g.
Velibeyrichia HENNINGSMOEN 1954
Hammariella n.g.
Hoburgiella n.g.
Juviella n.g.
Lophoctenella n.g.
Cryptolopholobus n.g.
Lauella n.g.
Grogarnia n.g.
Vinculoveliger n.g.
Berolinella n.g.
Dibolbina ULRICH & BASSLER 1923
Atterdagia n.g.
Macrypsilon n.g.

DIAGNOSIS.—*Beyrichiidae* in which the closing procedure in the dolonoid stage of the cruminal metamorphosis was much reduced or absent. Traces of the ancestral dolonoid flap, if present at all, are deflections or constrictions of the velar edge on the distal part of the crumina, and the closing of a dolonoid pouch never occurred; the tubulous velum was invaded and inflated more or less directly into a crumina.

REMARKS.—The crumina in a series of representative amphitoxotidine genera is shown in Figs. 98 and 99.

The derivation of this crumina from the craspedobolbinine type is evident. The crumina in the amphitoxotidine ancestors has passed through a phylogenetic development like that in *Leptobolbina*, and the traces of the dolonoid closing mechanism are reduced to a low tubercle or pit in or near the velar edge (Figs. 98A, C, and D; Figs. 99A, C, and F; Figs. 129B and C), often combined with a deflection of the velar edge on the crumina (best examples Figs. 98C–D and 129B), or reflected only in a deflection of the velar edge, as in *Amphitoxotis*.

There is no zygal ridge in the *Amphitoxotidinae*.

The other beyrichiid families permit a grouping of the species in genera with a very stable cruminal morphology. In the *Amphitoxotidinae*, on the contrary, the crumina can be quite different in species which show affinities

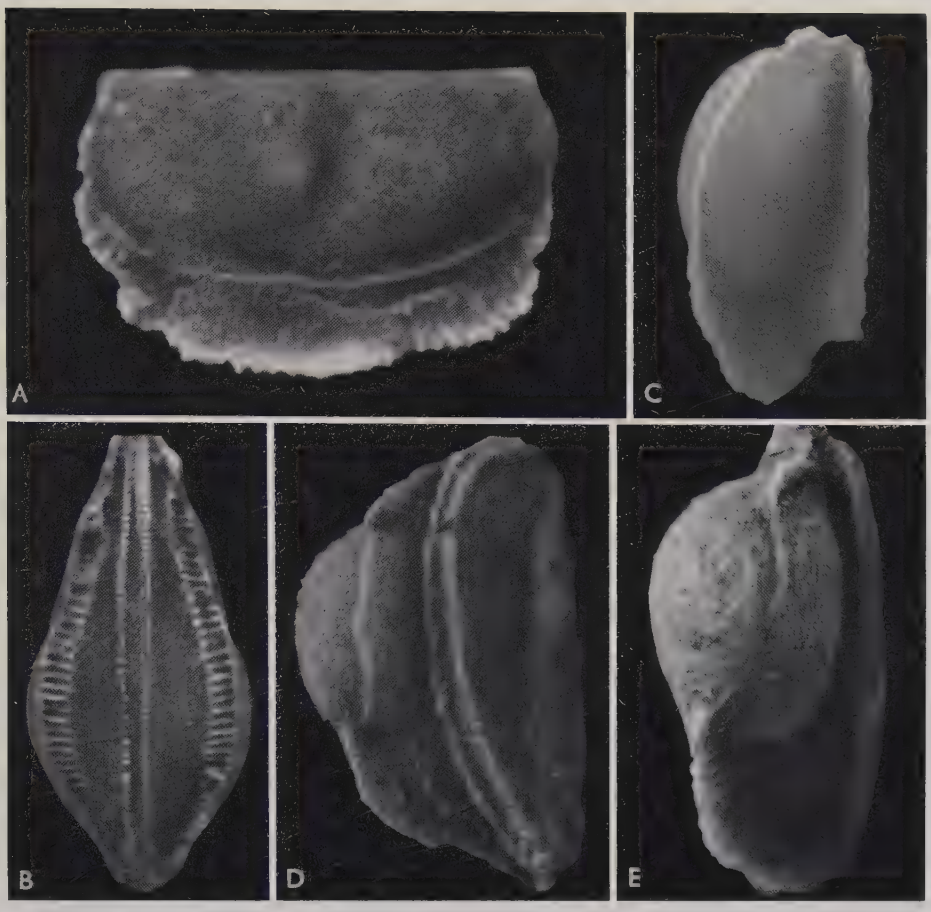


Fig. 100. Undescribed genera from the Wenlockian of Britain, illustrating the velar and cruminal morphology of the *Amphitoxotidinae*. ×40. A. From Wren's Nest, Dudley, Worcestershire, tecnomorph showing an almost entire velum with a basal crest of *Dibolbina–Berolinella* type. No. EW 6. B–C. From the south side of the Severn at Ironbridge, Shropshire, tecnomorphic carapace showing shape of the lumina in broken velar tubules (B, No. EW 8) and a discoidal crumina of *Berolinella* type, not occupying the entire width of the velum (C, No. EW 7) D. From road section at Harley Hill, Shropshire, No. EW 9. E. From Wren's Nest, No. EW 10.

in lobation and ornamentation. Most of the species, however, are so different in both lobation and cruminal morphology that it is impossible to associate one of this species more closely with any particular species than with others. The classificator is, then, faced with the choice of either grouping all these widely different species within *Sleia*, *Velibeyrichia*, and *Dibolbina* or of creating a large number of new genera, many of which must be monotypic. As there is already a large material at hand in addition to the material from Gotland and material best treated here together with the beyrichiids from Gotland, the grounds for choosing the latter alternative are very strong.

In connection with the description of the amphitoxotidine cruminal metamor-

phosis attention should be drawn to the figures shown by Swartz (1936, Pl. 87, figs. 8i–l) to illustrate the ventral morphology of a species identified with *Beyrichia moodeyi*, in which the deflection of the velar edge and the distinct traces of the ancestral closing mechanism can be observed. It is said in the illustration text that "it is clear that the female pouch is essentially a swollen part of the frill". This statement has been strongly confirmed.

Occurrence.—Silurian of Europe, Australia, and North America. No species are found on Gotland below the Ludlovian Hemse Beds, but in England the Wenlockian abounds in primitive amphitoxotidines (cf. Fig. 100).

Genus *Sleia* n.g.

Figs. 98 A–B and 101.

Derivation of the Name.—Latin *Sleius*, associated with Sles in Grötlingbo, Gotland.

Type Species.—*Sleia equestris* n.sp.

Species.—*Beyrichia Kochii* Boll 1862
Sleia equestris n.sp.
Sleia troglodytophila n.sp.
(Cf. also *Beyrichia cincta* Boll 1862, p. 223.)

Diagnosis.—Tuberculo-reticulate *Amphitoxotidinae* with a syllobial groove and a marked tubercle in the upper part of the sulcus near the hingeline. The velar edge forms a characteristic pattern derivable from two small bows on either side of the site of the apex of the ancestral dolonoid flap. Vertical marginal frill dissolved into a row of spines.

Remarks.—The genus *Sleia* shows clear affinities to other subfamilies. The velum is of a type very similar to that in *Craspedobolbina*, and it is known from atavistic specimens (cf. p. 223) that the cruminal metamorphosis begins with the extension of a dolonoid flap, but the formation of a dolonoid pouch and the insertion of the flap fails. It is known, too, that the cruminal opening originates through secondary perforation of a tissue layer which becomes calcified in atavistic specimens. The combination of tuberculosity or verrucosity and reticulation is unknown in other *Amphitoxotidinae* described but occurs in an undescribed genus from the Wenlockian of England. There is no other genus in the subfamily with a syllobial groove and calli. *Sleia* is, furthermore, the only amphitoxotidine genus in which calcarine tubercles or spines occur. Common features with the other amphitoxotidine genera are a very pronounced anteroventral depression and the absence of a zygal arch.

Sleia kochi (Boll 1862)

Fig. 4A.

1862 *Beyrichia Kochii* Boll (1862)—Boll, p. 121; Pl. I, fig. 2.
1954 *B. kochii* Boll 1862—Henningsmoen, p. 25 (referred to *Neobeyrichia* subg. n.)

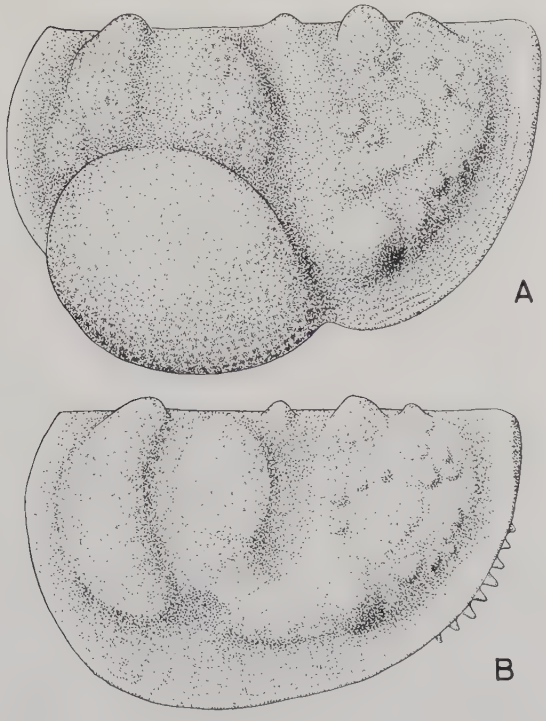


Fig. 101. *Sleia* n.g., drawing based on *Sleia equestris* n.sp. ×45. Ornamentation slightly simplified. A. Female. B. Male.

1957 *Neobeyrichia kochii* (Boll)—Kesling & Rogers, Pl. 127, figs. 8–9; Pl. 128, figs. 3–4.

Type Reference.—See above, pp. 19–20.

Remarks.—No very detailed description can be made from the tecnomorphic lectotype and extant figures. A differential diagnosis has to be given. *S. kochi* differs from the other two species by a narrower, more flange-like velum (the tubulosity, however, is distinctly discernible). The syllobial groove and the callus above it are more clearly distinguished in the somewhat fused tuberculation than in these species, and there are no pointed cusps protruding over the hingeline. There is no pointed, large calcarine tubercle in the female. The tubercle in the adductorial sulcus occupies a much larger part of the sulcus than in the other species. The velar edge on the crumina is undivided and probably very similar to that in *S. equestris*. The reticulation is largely effaced and passes over locally into a punctation.

Occurrence.—Silurian glacial erratics in northern Germany. An American *Sleia* species has been described by Copeland (1960) as *Beyrichia* (*Neobeyrichia*) *kochii*. It cannot be established from the only tecnomorphic specimen whether it is conspecific with *Sleia kochi*.

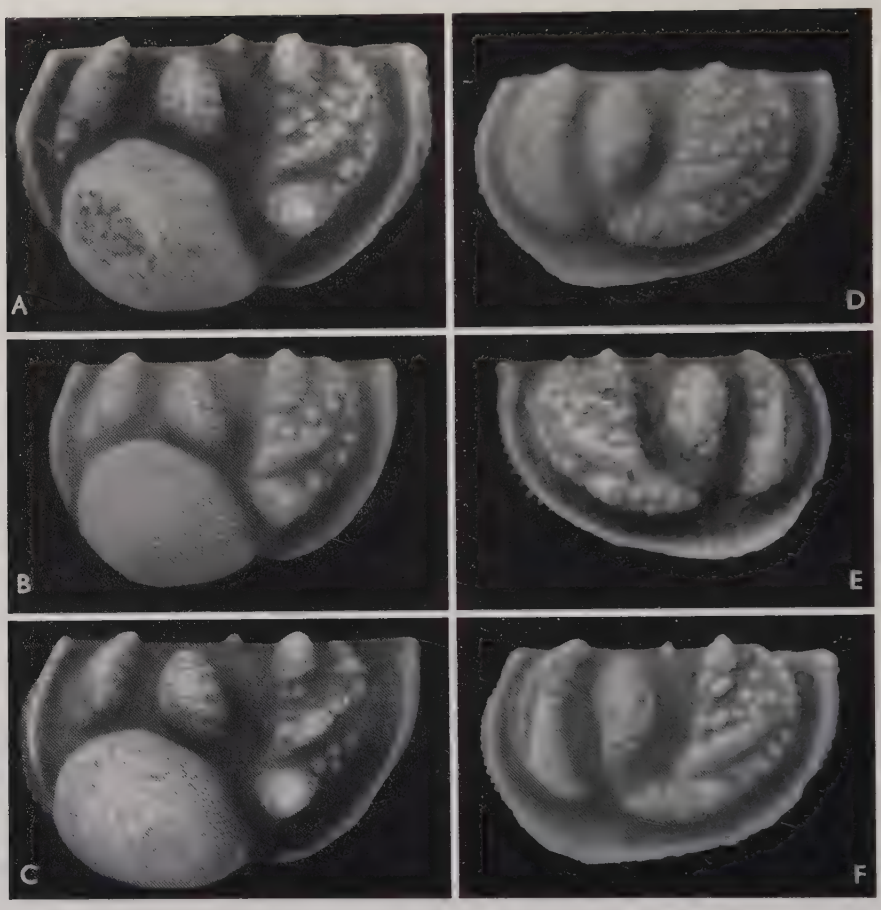


Fig. 102. *Sleia equestris* n.sp. × 30. A–C. Females. D–F. Tecnomorphs. A. Eke Beds, Lingvide, No. G 452. B. Hamra Beds, Sles, No. G 454 (holotype). C. Hamra Beds, Hoburgen I a, No. G 456. D. Eke Beds, Lau Backar, No. G 453. E. Hamra Beds, Sles, No. G 455. F. Hamra Beds, Sles, No. G 231.

Sleia equestris n.sp.

Figs. 36: 1–9, 42: 8, 102, and 103.

Derivation of the Name.—Latin *equestris*, associated with the horse, referring to the spur.

Holotype.—A left female valve, No. G 454 (Fig. 102 B).

Type Stratum and Type Locality.—Hamra Beds at Sles, Gotland.

Diagnosis.—*Sleia* species with a stout calcarine spine in the female. The velar edge forms a curve along the ventral side of the crumina, at mid-length curving round a small tubercle isolated from the edge.

Description.—Anterior lobe with a low cusp protruding over the hingeline, separated from the preadductorial node by a prenodal sulcus which is incon-

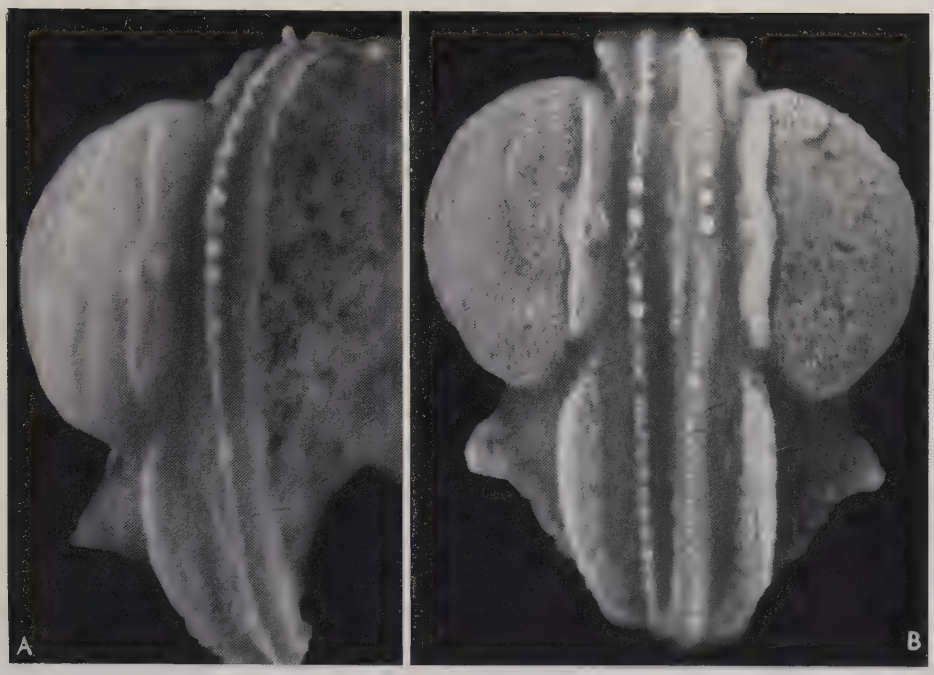


Fig. 103. *Sleia equestris* n.sp. Female specimens in ventral view, anterior end up. ×50. A. Right valve, Eke Beds, Lingvide, No. G 226. B. Carapace, Eke Beds, Ronnings, No. G 458.

siderably narrower than the adductorial sulcus. The syllobium has one larger anterior and one very small posterior cusp; the syllobial groove is very shallow, but the callus above it is well developed. Below the groove there is an enlarged calcarine tubercle in the male; in the female it is much larger and spur-like. The crumina is very large, almost round but slightly tapering towards its posterior junction with the velum; there are velar constrictions of the *Craspedobolbina* type on each side of the crumina. Reticulation somewhat distorted, noticeable especially on the lobal cusps, on the preadductorial node and on the tubercles or verrucae. These are evenly spread over the anterior lobe and on the preadductorial node; on the syllobium there is a slight differentiation into one field around the anterior cusp, one above the groove, containing the callus, and one below the groove, containing the calcarine tubercle or spine.

The exact shape of the velar ridge on the crumina mentioned in the diagnosis is best illustrated by figures (Figs. 103 A–B). The marginal structures and the torus are as stated for the genus.

Dimensions.—Hinge length–sulcal height of female specimens from Sles, in microns: 1565–960, 1450–905, 1385–880, 1350–860, 1345–880.

Remarks.—This species differs from *S. kochi* mainly by the presence of lobal cusps and a well developed calcarine spine; it differs from *S. troglody-*

Fig. 104. *Sleia troglodytophila* n.sp. Wenlock Shale, Wren's Nest, Dudley, Worcestershire. A. Female valve, No. EW 11 (holotype). × 30. B. Female valve, oblique ventral view, anterior end up, No. EW 12. × 50. C. Tecnomorph, No. EW 13. × 30.

tophila mainly by the general shape and ventral morphology of the crumina, and by the spur, cusps, and ornamentation of the syllobium.

Occurrence.—Hemse Beds: Botvide (very rare), Hulte (very rare). Eke Beds: Lau Backar (one tecnomorphic specimen in an enormous quantity of marl), Halor, Eke, Herrvide, Petsarve, Lingvide, Ronnings. Hamra Beds: Lunde, Sles, Hoburgen Ia, Hoburgen IIa, Hoburgen IIb. Sundre Beds: Juves. The species is by far the most dominant beyrichiid in the "*Sphaerocodium*" marls in the Eke and Hamra Beds in which the number of ostracode species is very small.

Sleia troglodytophila n.sp.

Fig. 104.

Derivation of the Name.—Latinized Greek *troglodytophilus*, companion of *Troglodytes*, the wren, alluding to the type locality.

Holotype.—A right female valve, No. EW 11 (Fig. 104A).

Type Stratum and Type Locality.—Wenlockian of Wren's Nest, Worcestershire, England.

Diagnosis.—*Sleia* species with a very large calcarine tubercle in the female. The velar edge on the crumina is divided into one shorter, straight, anterior portion and one longer, posterior portion, the anterior half of which is bent out from the anterior portion.

DESCRIPTION.—Both sulci almost equally broad; the lower end of the adductorial sulcus is separated from the prenodal sulcus and the anteroventral sulcus by the low connection (somewhat more marked than in the preceding species) between the preadductorial node and the syllobium; this connection has not the character of a zygal ridge. The syllobium has two rounded cusps, the anterior of them very prominent. The syllobial groove is shallow, and there is a callus above it; in the female there is a large, fairly rounded calcarine tubercle, and the callus is marked as an elevation between it and the anterior cusp. Ornamentation consisting of an almost entirely effaced reticulation; the sparse verrucosity is distinct only on the syllobium.

Torus near the velar edge. There are constrictions of the velum at its transitions into the crumina; the ventral morphology of the crumina is stated in the diagnosis; for details, cf. Fig. 104B. Vertical marginal structure consisting of a row of tubercles.

DIMENSIONS.—Hinge length–sulcal height of female valves from the type locality, in microns: 1410–900, 1380–850, 1345–825, 1345–805, 1300–825.

REMARKS.—This species differs from *S. equestris* mainly by the shape of the velar edge of the crumina and by the shape of the cusps and spur of the syllobium.

It is included here in order to show the considerable variation in the ventral morphology of the crumina which can occur within one genus and to demonstrate the fact that genera with a very limited number of species on Gotland may be represented by more species in other areas; there is one more, undescribed *Sleia* species from the Wenlockian at Wren's nest.

OCCURRENCE.—So far only at the type locality (abundant but difficult to prepare).

Genus *Hemsiella* n. g.

Figs. 99C, E, and 105.

DERIVATION OF THE NAME.—Feminine diminutive of Latin *Hemsius*, associated with, or inhabitant of, the parish of Hemse, Gotland, and the beds named after it.

TYPE SPECIES.—*Hemsiella loensis* n.sp.

SPECIES.—*Hemsiella hemsiensis* n.sp.
Hemsiella loensis n.sp.
Beyrichia Maccoyiana JONES 1855
Beyrichia Dalmaniana JONES 1855
Beyrichia hians BOLL 1856
Beyrichia elegans BOLL 1862
Hemsiella pulchricruminata n.sp.
Hemsiella anterovelata n.sp.

DIAGNOSIS.—Reticulate *Amphitoxotidinae* with more or less coherent an-

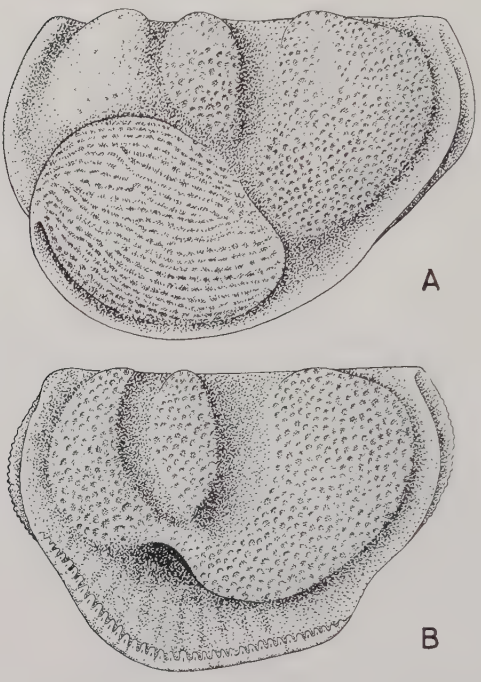


Fig. 105. *Hemsiella* n.g. Drawing based on *Hemsiella loensis* n.sp. from Lau Backar. × 50. A. Female. B. Male.

terior lobe, preadductorial lobe, and syllobium; the syllobium is broad. The velar edge, but not the torus (if present), continues uninterrupted across the crumina without deflections. Velum in the male with a denticulate border crest.

Remarks.—The first six of the species included form a very well defined group in which the velum continues as a ridge round the crumina but is obsolete in front of it; sometimes—especially in undescribed material from Scania—there is a small tubercular elevation in the velum on the most distal part of the crumina. In *H. pulchricruminata* and *H. anterovelata* the velum continues across the crumina and widens again in front of it; in *H. pulchricruminata* there is a small constriction of the velar edge on the most distal part of the crumina. A feature common to these species, which appears again in *Lophoctenella* and *Cryptolophobolus* but is unknown in more closely related genera, is the denticulate border crest in the males.

The Species from Silurian Erratics in Northern Germany.—A revision of the *Hemsiella* material from northern Germany would be too extensive to be included in the present paper. The lectotypes of four species described by Jones and Boll have been designated here; there is at least one undescribed species in the *Beyrichia* Limestone.

Some remarks should, however, be added in order to mark the distinction of the new species from Gotland from those in the North German material.

Hemsiella maccoyiana is a large species in which the syllobium is more or less dissected. There are forms with a very shallow depression below the rounded, protruding cuspidal part of the syllobium; in some forms, referred to as *Beyrichia maccoyiana sulcata* REUTER (cf. figures published by KESLING & ROGERS 1957), there is a deeper depression, and there is sometimes an additional, marked depression in the region where the syllobial groove is situated in other ostracodes. The denticles of the velar border crest are more densely spaced than in other species. There is a wide unornamented zone outside the velar ridge on the crumina; inside it there is a striation or reticulo-striation covering all the area between the ridge and the base of the crumina. The homogeneity of this species and its delimitation from *Hemsiella dalmaniana* —if there is any delimitation—still constitute an unsolved problem. *Hemsiella maccoyiana* is very finely reticulate, and a reticular pattern also covers the lateral side of the crumina.

Hemsiella dalmaniana (Fig. 2C) has a small reticulostriate field on the posteroventral part of the crumina which is otherwise completely smooth. There is a broad depression below the cuspidal part of the syllobium.

Hemsiella elegans has no traces of the reticulation, but the lateral side of the crumina is striate, without any direct traces of that reticular pattern from which the striation most certainly has originated. The cuspidal part of the syllobium does not protrude over the hingeline (Fig. 4C).

Hemsiella hians (Fig. 3D) is known from a tecnomorphic valve which proves the species to be associated with those mentioned above. It has the characteristic anteroventral undulation of the velum found in these species; some of the border denticles are preserved. The valve appears to be completely smooth, except for a faint verrucosity on the anterior lobe.

Some affinity to *Hemsiella* may also be traced in *Beyrichia cincta* BOLL 1862 (Fig. 4B). It has a very typical ornamentation of ridges laterally on the crumina and a small, callus-like ridge on the syllobium (cf. *Sleia*). Most probably it represents a new genus, known from one specimen without a type locality. Until new material is found in an autochthonous position or abundantly in erratics it is best placed among *Amphitoxotidinae incerti generis*.

Hemsiella loensis n.sp.

Figs. (105), 106, 107A, and 109D.

DERIVATION OF THE NAME.—Latin *Loensis*, from the parish of Lau, formed with the Old West Nordic stem *lǫ́*, a kind of meadow.

HOLOTYPE.—A left female valve, No. G459 (Fig. 106A and 107).

TYPE STRATUM AND TYPE LOCALITY.—Eke Beds at Lau Backar, Gotland.

DIAGNOSIS.—Distinctly and not very finely reticulate *Hemsiella* species. Syllobium entire. The lateral reticulation of the crumina stops abruptly at the outer limit of a smooth zone along the velar ridge; a similar zone inside the velar ridge is more or less well developed. No velum in front of the crumina.

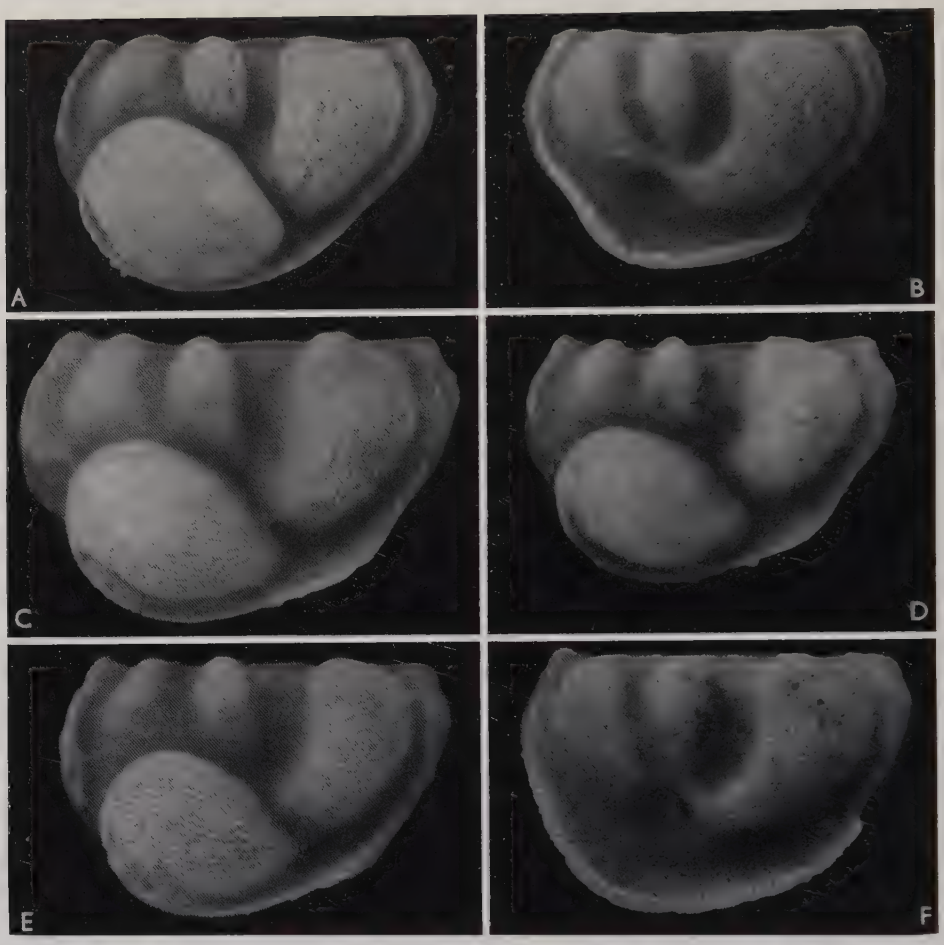


Fig. 106. *Hemsiella loensis* n.sp. ×40. A, C, D, and E females, B and F tecnomorphs. A. Eke Beds, Lau Backar, No. G 459 (holotype). B. Same locality, No. G 460. C–D. Hamra Beds, Sles, Nos. G 461 and G 462. E. Eke Beds, Halor, No. G 463. F. Eke Beds, Herrvide, No. G 464.

Description.—The reticulation covers all lobes except the most dorsal part of the anterior lobe where it is almost obsolete. The material from Lau Backar has a somewhat coarser reticulation than material from higher beds. The typical arrangement of the ornamentation along the velar edge is seen in Fig. 107A; the inner smooth zone is mostly less well developed than in the specimen figured. The male velum has the typical anteroventral undulation found in those species which lack a precruminal velar portion; posteroventrally it passes over in a curve or, more seldom, abruptly (Figs. 106B and F, Fig. 109D) into a velar ridge. The border denticles are between two and three for each tubule; anteroventrally and ventrally the tubulosity is very distinct. The posteroventral transition of the female velum into the posterior velar ridge is more or less

Fig. 107. Ventral morphology of the crumina in *Hemsiella* n.g. × 50. A. *Hemsiella loensis* n.sp. from Lau Backar, No. G 459. B. *Hemsiella hemsiensis* n.sp. from Hulte, No. G 466. The latter species shows some tendency to a thickening of the velum at the most distal point of the crumina; in *Hemsiella* material from Scania a low node may appear in this place.

rounded; in the extreme case the velar edge forms a straight line from the ridge on the crumina to the posterior velar ridge; in incident light the tubulosity is hardly to be traced. A faint torus is present even in the female but does not extend onto the crumina.

Dimensions.—Hinge length–sulcal height of female specimens in microns: Eke Beds, Lau Backar: 1100–765, 1030–705, 1010–700, 990–730, 965–700. Hamra Beds, Sles: 1220–900, 1190–780, 1025–765, 1000–780, 990–800 (see also size dispersion diagram, Fig. 116).

Remarks.—This species differs from *H. hemsiensis* by its coarser reticulation and the well delimited smooth zone or zones along the velar ridge on the crumina.

Occurrence.—Eke Beds: Lau Backar, Halor, Herrvide, Ronnings. Hamra Beds: Lunde, Sles, Hoburgen Ia, Hoburgen IIa, Hoburgen IIb.

Hemsiella hemsiensis n.sp.

Figs. 107B and 108.

Derivation of the Name.—Latin *Hemsiensis*, from the parish of Hemse in which the type locality is situated.

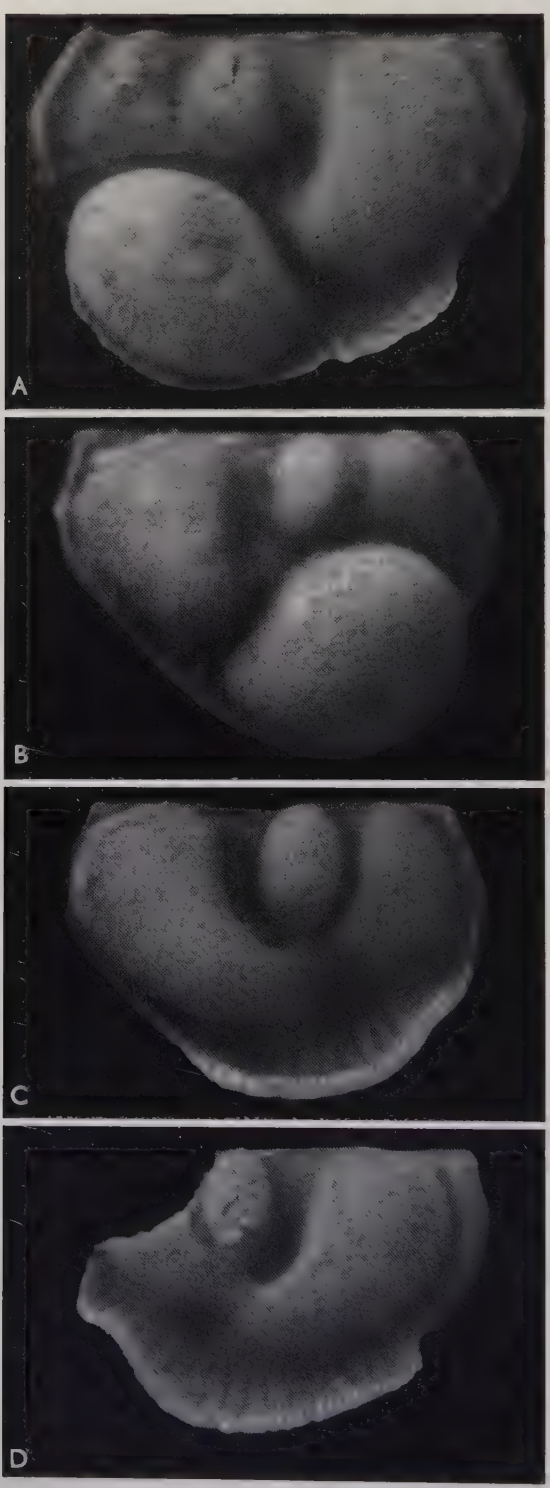


Fig. 108 A. *Hemsiella hemsiensis* n.sp., Hemse Beds, Hulte. Female valve, No. G 467 (holotype). × 40.

Fig. 108 B. Same species and locality. Female valve, No. G 468. × 40.

Fig. 108 C. Same species and locality. Tecnomorphic valve, No. G 469. × 40.

Fig. 108 D. Same species and locality. Tecnomorphic valve, No. G 470. × 40.

HOLOTYPE.—A left female valve, No. G467 (Fig. 108A).

TYPE STRATUM AND TYPE LOCALITY.—Hemse Beds at Hulte, Gotland.

DIAGNOSIS.—*Hemsiella* species with extremely fine reticulation on the lobes. Syllobium entire. The lateral and ventral reticulation of the crumina becomes gradually finer towards the velar ridge on the crumina, and there is no distinct smooth zone along this ridge. No velum in front of the crumina.

DESCRIPTION.—All lobal and adventral features agree well with the description of the preceding species. The ornamentation lies, however, far beyond the variational range of *H. loensis*. The reticulation of the lobes is so fine that it is difficult to discern it even with the scale used in Fig. 108. There is no smoother field near the top of the anterior lobe. The cruminal reticulation, however, is very similar to that in *H. loensis*; laterally it is coarse and has a pronounced tendency to pass over into a striation, ventrally this tendency becomes more pronounced near the velar ridge.

DIMENSIONS.—Hinge length–sulcal height of female valves from the type locality: 1385 μ – 1145 μ, 1318 μ – 1045 μ.

REMARKS.—Except for the considerably larger size, this species differs from *H. loensis* by the very fine lobal reticulation and the morphology along the velar ridge on the crumina.

OCCURRENCE.—Hemse Beds: Hulte, Leisungs.

Hemsiella pulchricruminata n.sp.

Figs. 109A–C.

DERIVATION OF THE NAME.—Latin *pulchricruminatus*, provided with a beautiful crumina.

HOLOTYPE.—A left female valve, No. G471 (Fig. 109A and C).

TYPE STRATUM AND TYPE LOCALITY.—Hemse Beds at Tänglings, Gotland.

DIAGNOSIS.—*Hemsiella* species with velar edge passing across the crumina, widening both in front of and behind it. The anteroventral half of the crumina is striate, lateroventrally even coarsely reticulate.

DESCRIPTION.—Lobal arrangement as stated for the genus. The male velum has a border denticulation like that in all other *Hemsiella* sp.; there is no anteroventral undulation of the velum. Velum in both sexes abruptly restricted posteroventrally. On the most distal part of the crumina the velum is interrupted by a very small constriction. All the subvelar part of the female carapace is finely striate; the crumina is ornamented as stated in the diagnosis; all lobes are finely and evenly reticulate.

DIMENSIONS.—Hinge length–sulcal height of female valves from the type locality, in microns: 880–640, 865–705, 850–665, 840–630, 830–670.

REMARKS.—This species has obvious affinities with *H. anterovelata* but differs from it by the very narrow velar ridge on the crumina and by the lateral ornamentation of the crumina.

OCCURRENCE.—Hemse Beds: Tänglings, Sigvalde.

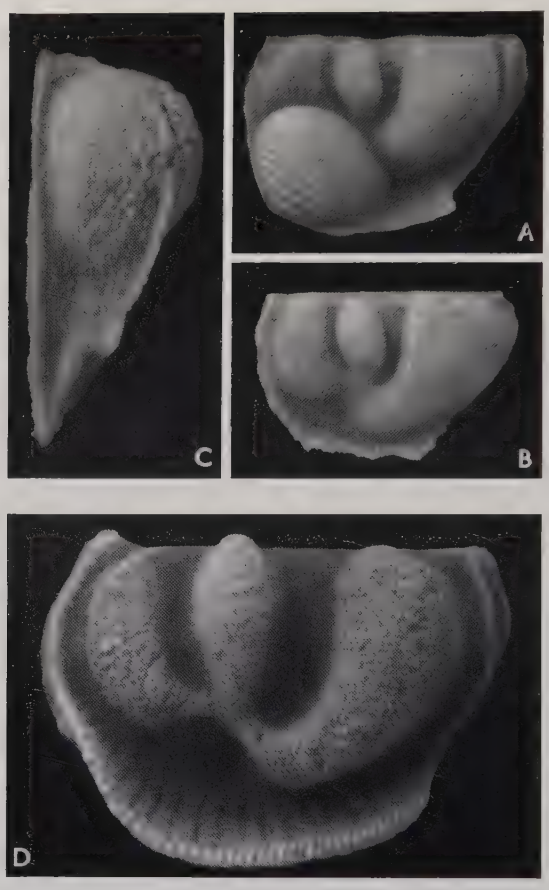


Fig. 109. A–C. *Hemsiella pulchricruminata* n.sp., Hemse Beds, Tänglings. A and C. Female valve, No. G 471 (holotype), in lateral view (A, ×40) and ventral view (C, anterior end up, ×60). B. Tecnomorphic valve, No. G 472. ×40. D. *Hemsiella loensis* n.sp., Hamra Beds, Hoburgen I a, tecnomorph showing reticulation in the same magnification (×40) as Fig. 108. No. G 473.

Hemsiella anterovelata n.sp.

Fig. 110.

Derivation of the Name.—Latin *anterovelatus*, provided with an anterior (portion of the) velum.

Holotype.—A left female valve, No. G474 (Fig. 110A).

Type Stratum and Type Locality.—Eke Beds at Lau Backar, Gotland.

Diagnosis.—*Hemsiella* species with velum continued as an uninterrupted frill across the crumina; lateral part of the crumina reticulate.

Description.—Lobation as stated for the genus. The velum is very wide, with a densely denticulate border crest in the male, distinctly tubulous in both sexes. There is no anteroventral undulation in the male velum. In both sexes there is an abrupt constriction of the velum posteroventrally; posteriorly it continues only as a low ridge (as in all other *Hemsiella* species). Cruminal morphology as stated in the diagnosis cf. Fig. 110D. All lobes finely reticulate; crumina finely reticulate laterally, with the meshes in the reticulation extended lengthwise on the crumina. The entire ventral side of the valve, including the

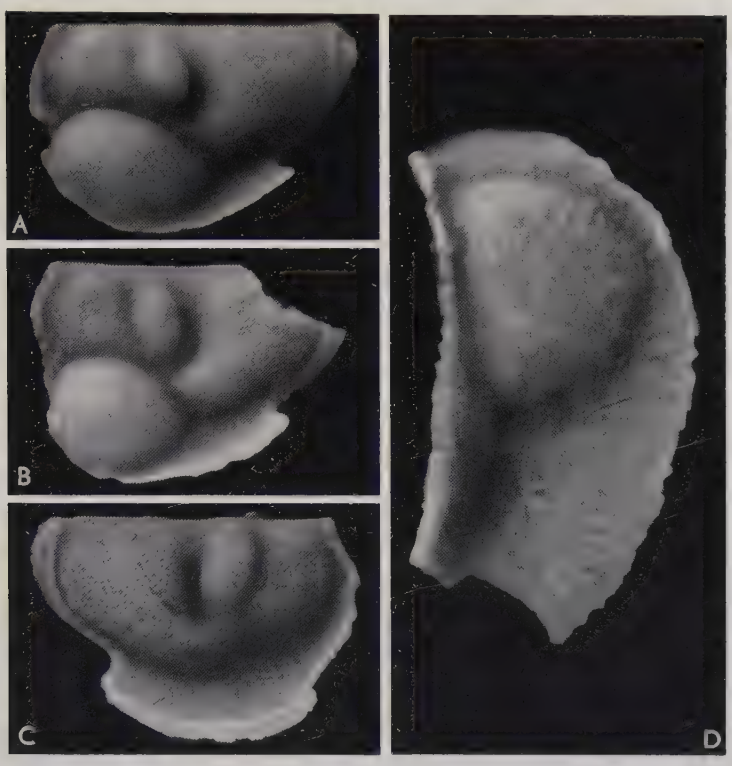


Fig. 110. *Hemsiella anterovelata* n.sp. A–C. From the Eke Beds at Lau Backar. ×40. A. Female valve, No. G 474 (holotype). B. Female valve, No. G 475. C. Male valve, No. G 477. D. Oblique ventral view of valve fragment with well preserved velum and crumina (anterior end up), showing incomplete occupation of the velum by the crumina. No. G 476. Sles. ×60.

velum, is finely striate, with traces of the original reticulation on the crumina; outer side of the velum finely striate which gives the tubules a wrinkled appearance.

Dimensions.—Hinge length–sulcal height of female specimens from Sles: 1030 μ – 785 μ, 985 μ – 765 μ, 960 μ – 770 μ, 930 μ – 745 μ.

Remarks.—This species is closely related to *H. pulchricruminata* but differs from it by the morphology of the cruminal part of the velum and the lateral ornamentation of the crumina.

Occurrence.—Eke Beds: Lau Backar (very rare). Hamra Beds: Sles.

Genus *Amphitoxotis* n.g.

Figs. 98E and 111.

Derivation of the Name.—Greek ἀμφί, both sides, and τοξότις, woman archer, alluding to the shape of the velar ridge on the crumina.

Type Species.—*Amphitoxotis curvata* n.sp.

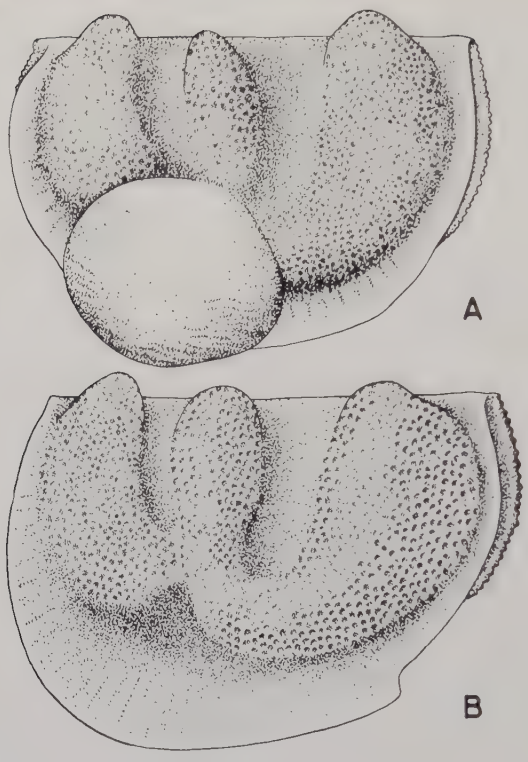


Fig. 111. *Amphitoxotis* n.g. Drawing based on *Amphitoxotis curvata* n.sp. ×60. A. Female. B. Male.

Species.—Only the type species.

Diagnosis.—*Amphitoxotidinae* with wide velum, even in front of the crumina, more or less abruptly interrupted posteroventrally. Velar edge across the velum strongly deflected in marginal direction. Torus not extending onto the crumina.

Amphitoxotis curvata n.sp.

Fig. 112.

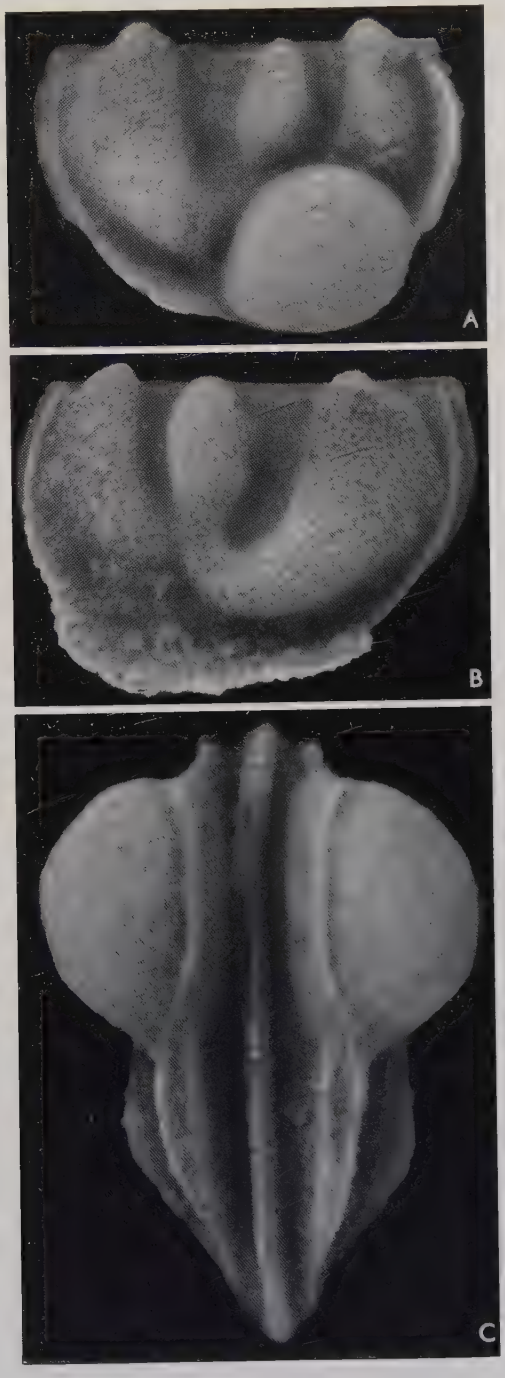
Derivation of the Name.—Latin *curvatus*, curved, alluding to the shape of the velar ridge on the crumina.

Holotype.—A female carapace, No. G478 (Figs. 112A and C).

Type Stratum and Type Locality.—Hemse Beds at Snoder, Gotland.

Diagnosis.—As for the genus.

Description.—The anterior lobe is narrow, protruding with a rounded cusp over the hingeline. The prenodal sulcus is only half as wide as the adductorial sulcus; it does not cut through the connection between the anterior and the preadductorial lobes completely. The latter lobe also communicates with the syllobium which protrudes over the hingeline with a cusp; the general



A. Female carapace, No. G 478 (holotype) × 40.

B. Tecnomorph, No. G 479. × 40.

C. The holotype (No. G 478) in ventral view, anterior end up. × 50.

Fig. 112. *Amphitoxotis curvata* n.sp., Hemse Beds, Snoder.

shape of the lobes and sulci is seen in Fig. 112. The velum is very wide in the male, lacking a denticulate border crest; posteroventrally it passes abruptly over into a velar ridge. Both the precruminal and postcruminal portions of the velum are developed in the female; they are narrower than the male velum but show a distinct tubulosity. The velar edge can be followed across the crumina as stated in the diagnosis; a torus is developed near the edge of the postcruminal velar portion of the velum but becomes obsolete at the posterior part of the crumina (Fig. 112C). All lobes are evenly covered with an even, medium fine reticulation; the crumina has traces of a fine reticulation.

Dimensions.—Hinge length–sulcal height of female valves from the type locality: 1400 μ – 1030 μ, 1365 μ – 980 μ. Same measurements on material from Petes: 1730 μ – 1220 μ, 1630 μ – 1280 μ.

Occurrence.—Hemse Beds: Eske, Snoder, Petes.

Genus *Velibeyrichia* Henningsmoen 1954

Remarks.—The cruminal morphology of this genus is unknown. *Velibeyrichia* differs from all other known amphitoxotidine genera in having a tubulous, unrestricted velum all round the free edge. It differs further from *Hoburgiella*, the only genus which might be considered as associated with it according to velar characters, by its extremely broad preadductorial lobe, the broad anterior lobe, and the broad syllobium; none of these units, which fill out the valve surface down to the base of the velum, protrude over the hingeline.

The species referred to *Beyrichia moodeyi* discussed by Swartz 1936 (Pl. 78, figs. 8i–l) is not identical with the type species of this family. It has a restricted velum—very abruptly restricted in the male—and quite different proportions of the lobes; even without knowing the female of the specimen figured by Ulrich & Bassler 1923, Pl. LXIII, fig. 27, and its cruminal morphology it is difficult to regard them as being congeneric.

Genus *Hammariella* n. g.

Figs. 99G and 113.

Derivation of the Name.—Latin *Hammarius*, associated with the region of Stora and Lilla Hammars (and Hammarudden), referring to the type locality of the type species.

Type Species.—*Hammariella pulchrivelata* n.sp.

Species.—Only the type species.

Diagnosis.—*Amphitoxotidinae* with very broad anterior lobe and syllobium and narrow sulci. Velum very wide, abruptly cut off posteroventrally, continued posteriorly only by a velar bend. Crumina very large, without traces of a torus or of the velar edge. No velar frill in front of the crumina.

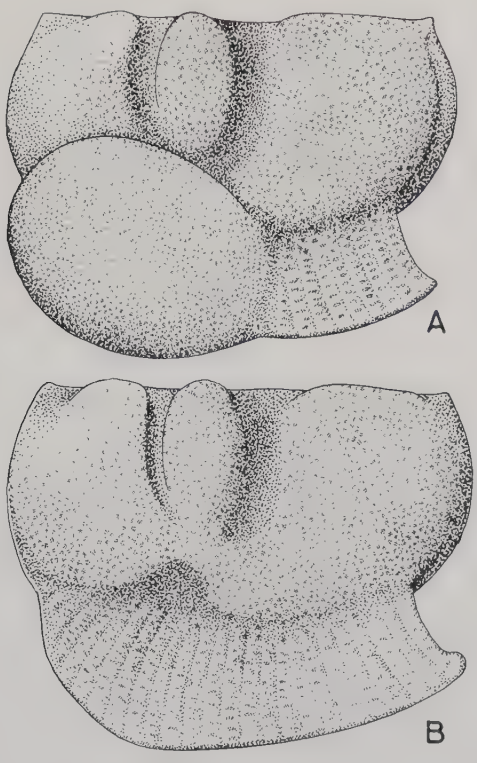


Fig. 113. *Hammariella* n.g. Drawing based on *Hammariella pulchrivelata* n.sp. Ornamentation slightly simplified. ×45. A. Female. B. Male.

Hammariella pulchrivelata n.sp.

Figs. (113), 114, and 115.

Derivation of the Name.—Latin *pulchrivelatus*, provided with a beautiful velum.

Holotype.—A right female valve, No. G482 (Fig. 114B).

Type Stratum and Type Locality.—Hemse Beds at Hammarudden, Gotland.

Diagnosis.—As for the genus.

Description.—The anterior lobe is very broad, occupying all the space between the base of the velum and the prenodal sulcus which is very narrow. The sulci do not isolate the preadductorial node from the anterior lobe and the syllobium. The adductorial sulcus is comparatively narrow but wider than the prenodal sulcus. The syllobium is very broad and has no protruding dorsum or dorsal cusp. There is a very marked anteroventral depression.

In the male the wide velum begins at the most anterior point of the carapace and widens very rapidly to attain its greatest width anteroventrally. Posteroventrally it is abruptly cut off along the last tubule which is slightly thicker

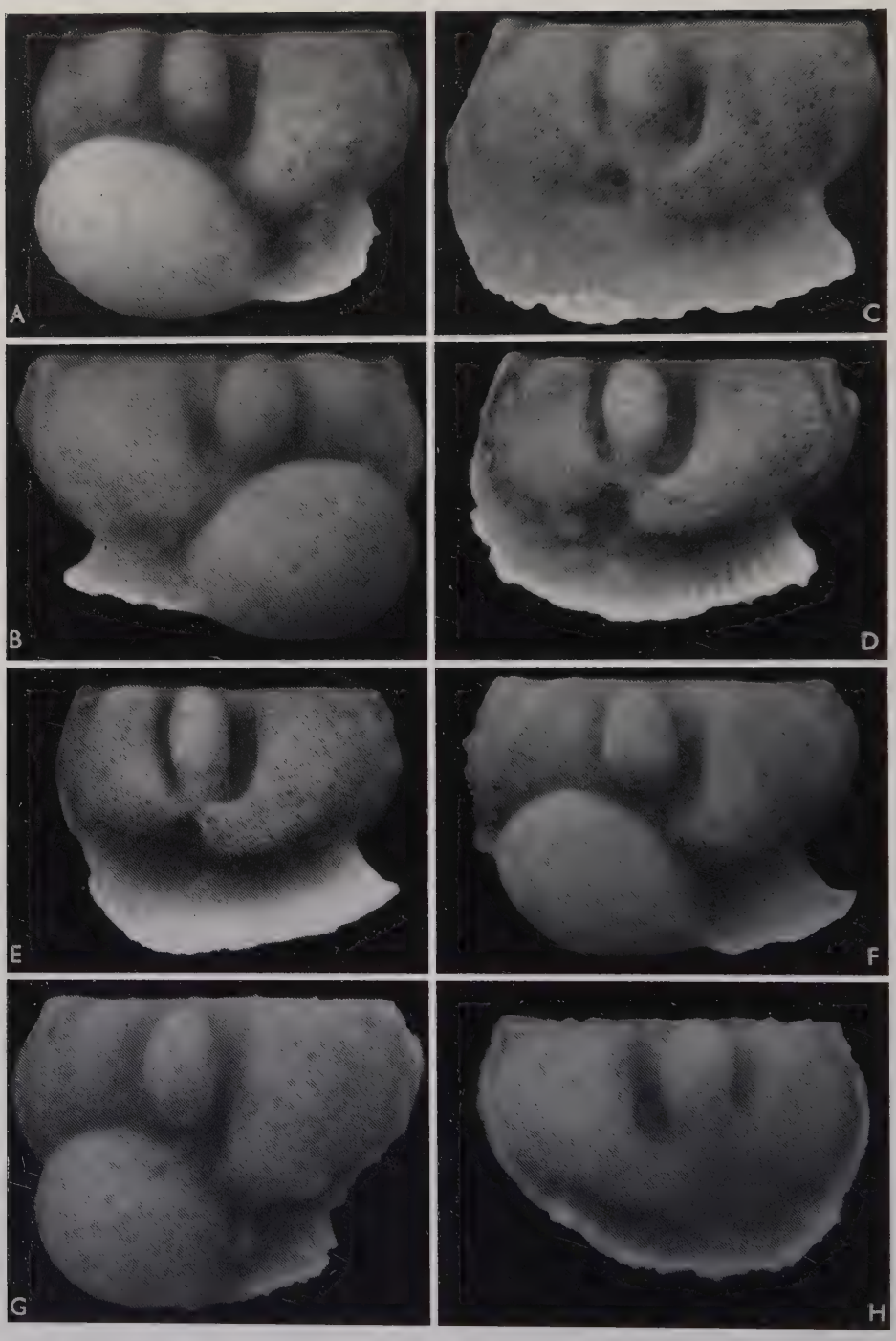


Fig. 114. *Hammariella pulchrivelata* n.sp., Hemse Beds. ×40. A–E from Hammarudden, F from Tänglings, and G and H from Tjängdarve. (see further data on opposite page).

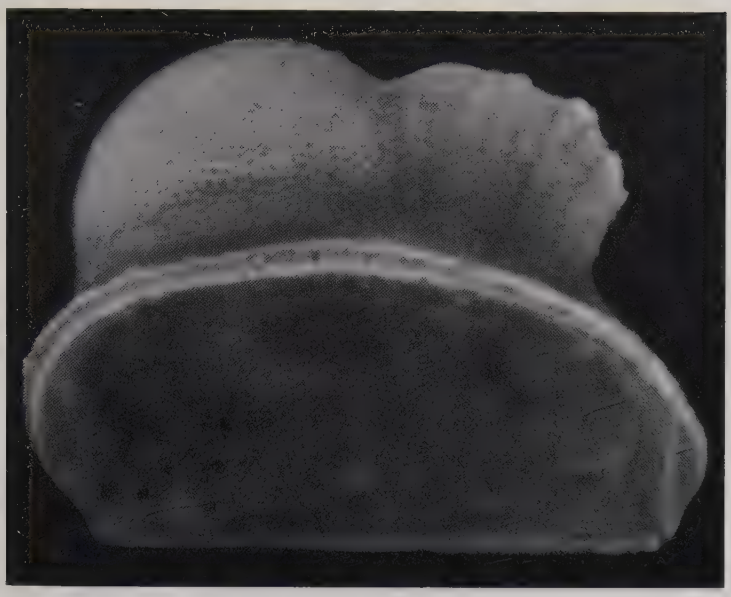


Fig. 115. *Hammariella pulchrivelata* n.sp. Oblique ventral view of a left female valve (anterior end to the left), showing velar and cruminal morphology. No. G 488. Hammarudden. ×75.

than the others in the velum. The posterior limitation of the velum in well preserved specimens is somewhat concave. Other parts of the velum are marked only as velar bends. There is no torus behind the crumina.

All lobe surfaces and all sides of the crumina are finely reticulate; the only differentiation in the pattern is on the dorsal part of the anterior lobe where the reticulation is more or less effaced. The ornamentation of both sides of the velum can be described as reticulo-striate (cf. Fig. 115); the transition towards the crumina is very gentle, and at some distance from it the striation gives the velum the wrinkled appearance which is typical of many amphitoxotidines and craspedobolbinines.

Dimensions.—Hinge length–sulcal height of female specimens from Hammarudden, in microns: 1060–765, 1030–790, 1005–865, 990–805 (see also a size dispersion diagram, Fig. 116). Female specimens from Tjängdarve: 1045–865, 1040–900, 1010–805, 930–765.

Occurrence.—Hemse Beds: Hammarudden, Skåne, Hammars, Fie, Hägvide, Medbys, Tjängdarve, Amlings.

Fig. 114 (opposite page) *Hammariella pulchrivelata* n.sp. A. Female, No. G 480. B. Female, No. G 482. C. Male, No. G 481. D. Tecnomorph, No. G 483. E. Tecnomorph, No. G 484. F. Female, No. G 485. G. Female, No. G 486. H. Tecnomorph, No. G 487. (Localities stated on opposite page.)

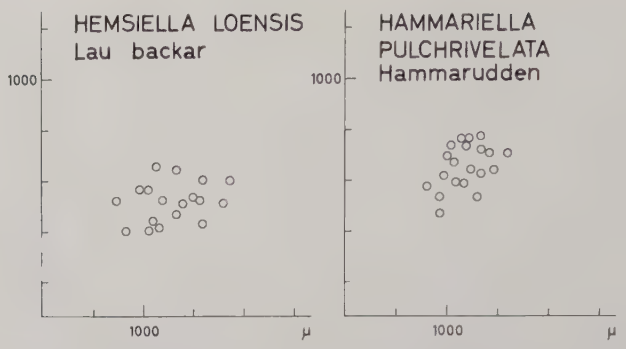


Fig. 116. Size dispersion of female specimens of *Hemsiella loensis* n.sp. and *Hammariella pulchrivelata* n.sp. in closed samples from the localities stated.

Genus *Hoburgiella* n.g.

Figs. 99A and 117.

Derivation of the Name.—Feminine diminutive of Latin *Hoburgius*, associated with Hoburgen on southernmost Gotland.

Type Species.—*Hoburgiella tenerrima* n.sp.

Species.—Only the type species.

Diagnosis.—*Amphitoxotidinae* with narrow syllobium and a wide velum

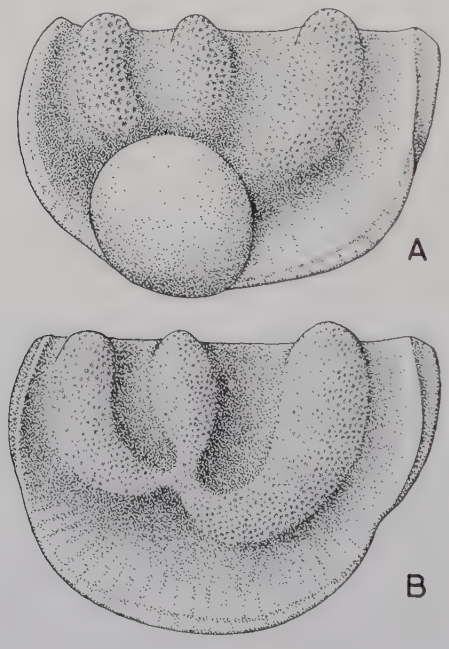


Fig. 117. *Hoburgiella* n.g. Drawings based on *Hoburgiella tenerrima* n.sp. ×45. A. Female. B. Male.

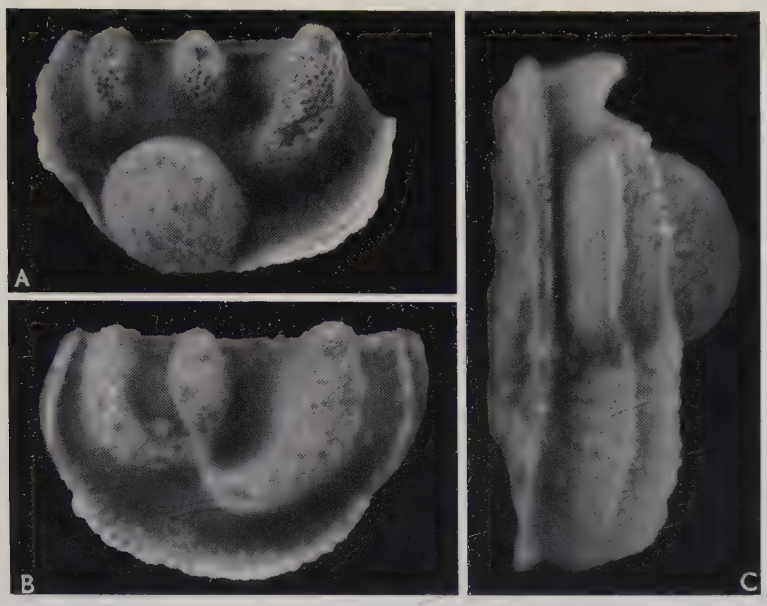


Fig. 118. *Hoburgiella tenerrima* n.sp., Hamra Beds, Hoburgen I a. A. Female valve, No. G 489. × 40. B. Male, No. G 490. × 40. C. The holotype (No. G 489) in ventral view (anterior end up). × 60.

which is inconsiderably restricted posteroventrally. The velar edge passes across the crumina; there is a well developed precruminal portion of the velum. Parallel to the velar edge and not very widely separated from it is a sharp toric ridge along the postcruminal portion of the velum and across the crumina.

Hoburgiella tenerrima n.sp.

Fig. 118.

Derivation of Name.—Feminine superlative of Latin *tener*, fine, delicate, referring to the general appearance of the carapace.

Holotype.—A left female valve, No. G 489 (Fig. 118A, C).

Type Stratum and Type Locality.—Hamra Beds at Hoburgen Ia, Gotland.

Diagnosis.—As for the genus.

Description.—All three lobes about equally narrow—the syllobium is somewhat wider—united by very narrow connections below the preadductorial lobe. Sulci about as wide as the anterior and preadductorial lobes; anteroventral depression very deep. Velum wide, tubulous; posteroventrally, or even posteriorly, there is a gentle restriction of the velum, more pronounced in the male. There is a border crest on the outside of the velum and near its edge; it is present in both sexes and is not denticulate. The crumina is almost perfectly globular; its ventral morphology is described in the generic diagnosis; cf. Fig. 118C. The lobes are finely and evenly reticulate.

Dimensions.—Hinge length—sulcal height of female valves:

Hemse Beds, Hulte: 951 μ–730 μ. Hamra Beds; Hoburgen 1090 μ–1065 μ, 1020 μ–920 μ.

Occurrence.—Hemse Beds: Tänglings, Hulte. Burgsvik Beds: Husryggen. Hamra Beds: Lunde, Hoburgen Ia, Hoburgen IIa, Hoburgen IIb. Sundre Beds: Juves.

Genus *Juviella* n.g.

Fig. 99F.

Derivation of the Name.—Feminine diminutive of a Latin adjective *Juvius*, associated with the locality of Juves.

Type Species.—*Juviella juvensis* n.sp.

Species.—Only the type species.

Diagnosis.—*Amphitoxotidinae* with only a very low connection between the anterior and preadductorial lobes. All lobes narrow. Velar edge constricted behind the crumina, not extending onto it; there is no precruminal velar frill. A toric ridge continues in a characteristic bow across the inner ventral part of the crumina.

Juviella juvensis n.sp.

Fig. 119.

Derivation of the Name.—Latin *Juvensis*, inhabitant of Juves, formed on the stem *juv-* in the name of the type locality.

Holotype.—A left female valve, No. G 491 (Fig. 119A).

Type Stratum and Type Locality.—Sundre Beds at Juves, Gotland.

Diagnosis.—As for the genus.

Description.—Lobes narrow, sulci wide; the width of the syllobium is less than twice the width of the narrow anterior lobe. The anteroventral depression is very deep, separated from the prenodal sulcus by only a very low lobal connection. The connection between the preadductorial lobe and the syllobium is also comparatively low but distinct, and the ornamentation on this connecting ridge is never effaced. The lateral surfaces of the lobes are flattened and finely reticulate, but the syllobium always shows tendencies to become dissected, generally by a narrow, obliquely transversal depression (Fig. 119A); in the extreme case there is almost a lobular differentiation implying that the cuspidal and ventral parts of the syllobium are separated from the middle part by marked depressions; a faint verrucosity may also be observed. All lobes protrude over the hingeline.

The male velum is tubulous but not very wide, with a slight restriction posteroventrally; no border crest has been observed. The female velum is frill-like only in the postcruminal portion; it is constricted behind the crumina and forms a short, wing-like structure (Fig. 119B).

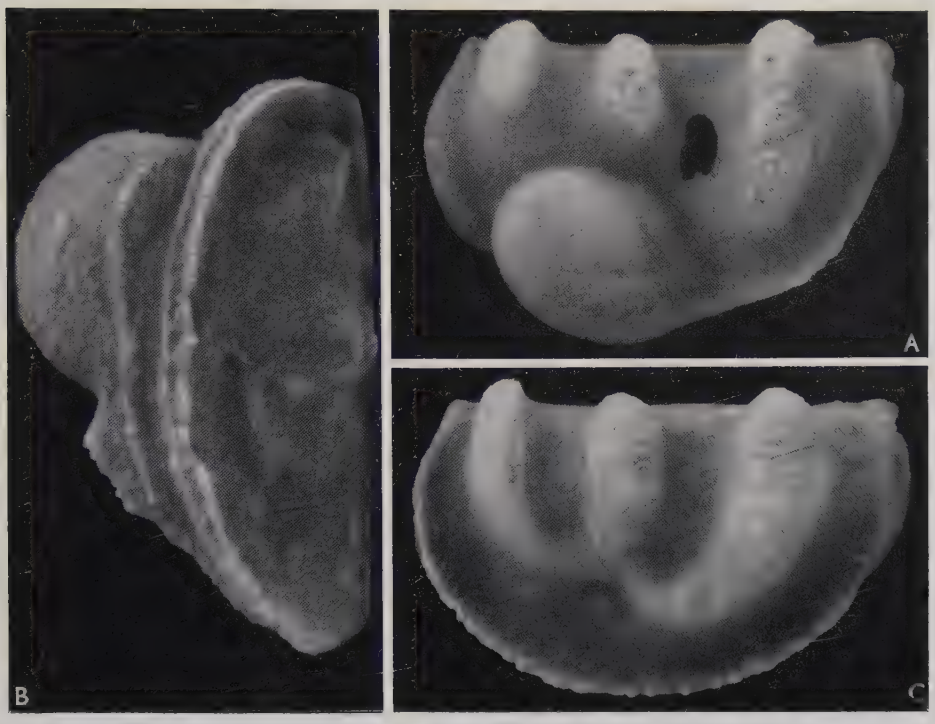


Fig. 119. *Juviella juvensis* n.sp., Sundre Beds, Juves. A. Female valve, No. G 491 (holotype). ×40. B. Female valve in oblique ventral view (anterior end up), No. G 492. ×60. C. Male valve, No. G 493. ×40.

Dimensions.—Hinge length—sulcal height of female valves from Juves: 1500 μ–1000 μ, 1480 μ–845 μ, 1430 μ–870 μ, 1320 μ–800 μ.

Occurrence.—Hamra Beds: Hoburgen Ia, Hoburgen IIa. Sundre Beds: Juves.

Genus *Lophoctenella* n. g.

Figs. 98G and 120.

Derivation of the Name.—Derived from Greek κτείς, comb, and λόφος, a coil of hair, referring to the border crest of the velum and the arrangement of the cristal loops.

Type Species.—*Lophoctenella angustilaqueata* n.sp.

Species.—*Lophoctenella angustilaqueata* n.sp.

Beyrichia scanensis Kolmodin 1869

Diagnosis.—*Amphitoxotidinae* with a strongly reduced anterior lobe and long narrow cristal loops on the preadductorial lobe and the syllobium. Denticulate border crest along all the anterior and ventral parts of the male velum. The velar edge and the torus both continue parallel to each other across the crumina.

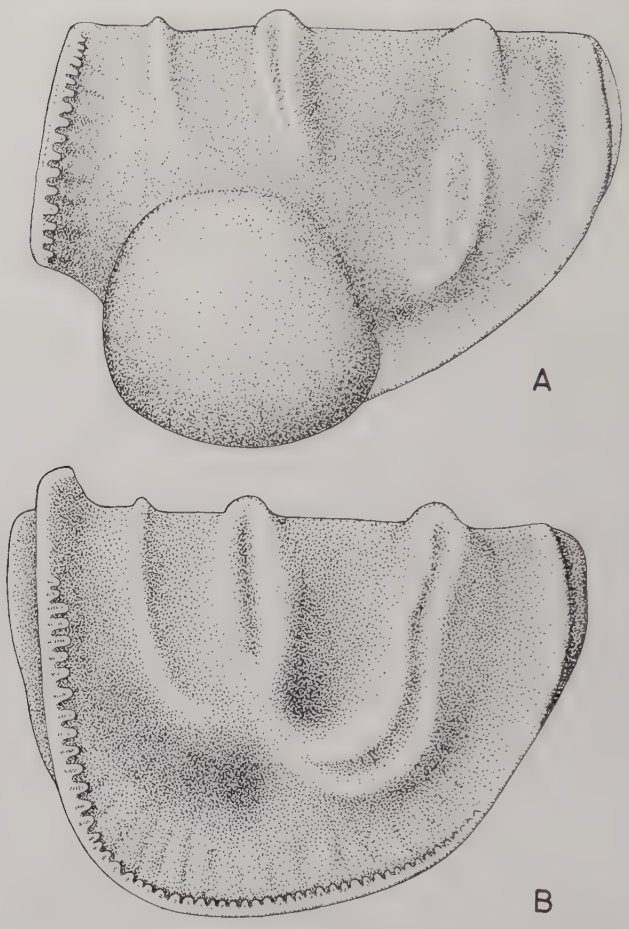


Fig. 120. *Lophoctenella* n.sp. Drawing based on *Lophoctenella angustilaqueata* n.sp. ×45. A. Female. B. Male.

Remarks.—The difficulty of obtaining sufficient material of both dimorphs makes it hard to estimate the actual number of *Lophoctenella* species in the material from Scania and North Germany; probably there is one additional species in each area.

Lophoctenella angustilaqueata n.sp.

Fig. 121.

Derivation of the Name.—Latin *angustus*, narrow, and *laqueatus*, provided with a loop.

Holotype.—A right female valve, No. G 494 (Fig. 121 A).

Type Stratum and Type Locality.—Hamra Beds at Hoburgen I a, Gotland.

Diagnosis.—*Lophoctenella* species with very narrow velar loops; the syllobial

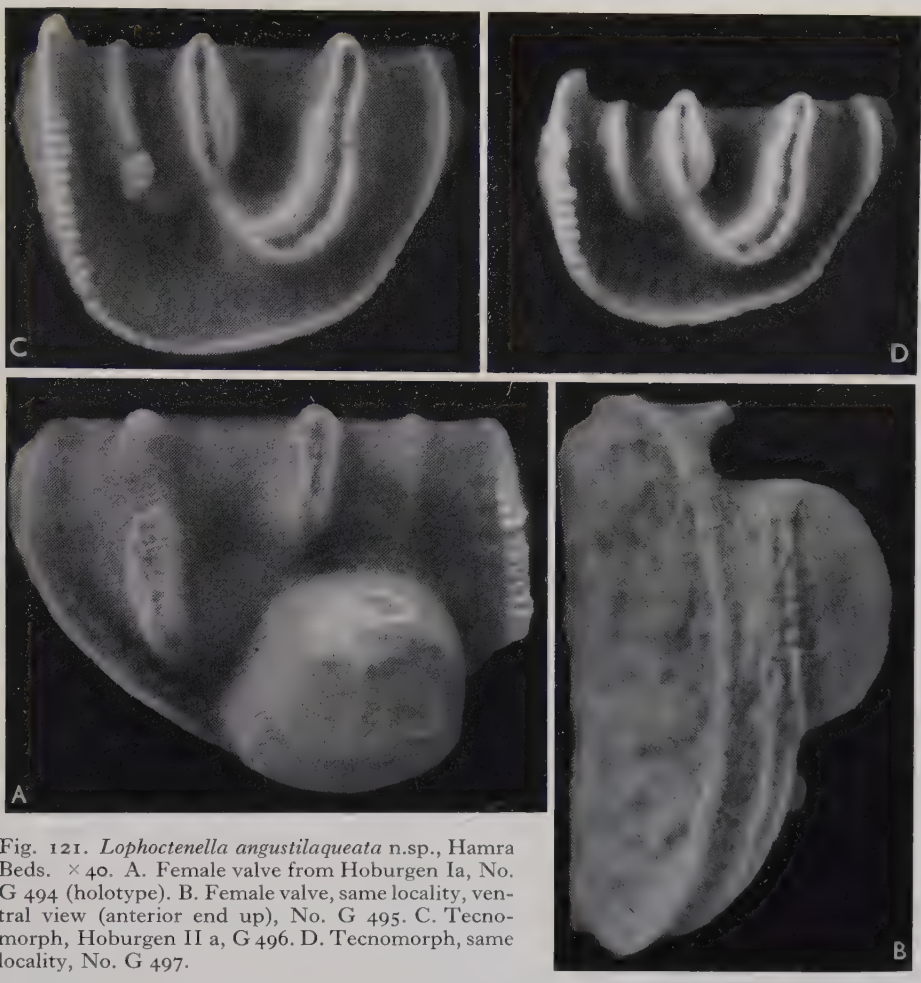


Fig. 121. *Lophoctenella angustilaqueata* n.sp., Hamra Beds. ×40. A. Female valve from Hoburgen Ia, No. G 494 (holotype). B. Female valve, same locality, ventral view (anterior end up), No. G 495. C. Tecnomorph, Hoburgen II a, G 496. D. Tecnomorph, same locality, No. G 497.

loop is well marked right onto the syllobial cusp. The anterior lobe in the female is strongly reduced; the loop-like character of the ornamentation of the syllobium and preadductorial lobe is discernible even in the female.

Description.—The dimorphism in this and associated species comprises almost every part of the carapace, and males and females have to be described separately.

The male carapace is very deep. The anterior lobe is strongly reduced, ridge-like, and distinctly separated from the other lobes above the deep anteroventral depression. The most prominent parts of the syllobium and the preadductorial lobe are completely crowned by the narrow cristal loops; the lumen in the loops is as narrow as the cristae bordering it; there is also a narrow cristal connection between the two loops (Figs. 121 C–D). All lobes protrude over the hingeline. The denticulate border crest begins a little below the anterior end of

the velum and continues to the posteroventral part of the carapace; the denticulation is most pronounced anteriorly. The parts of the velum inside the denticulation are distinctly tubulous; posteriorly there is a velar ridge. The anterior part of the velar edge forms an angle of 90°, or slightly less, with the hingeline.

The lobation in the female is considerably different. The anterior lobe is still more suppressed, and the preadductorial lobe is bent backwards by the inflation of the crumina. The syllobium is divided by a depression into a cuspidal part and a main, lower part; the latter part and the preadductorial lobe have cristal loops which are considerably less marked than in the male. The velum forms an angle of 90° or slightly more with the anterior part of the hingeline. The anterior part of the velum is denticulate and is separated from the crumina by a wide constriction. Cruminal morphology as in the generic diagnosis, cf. Fig. 121 B. Behind the crumina the velum is more flange-like, without a denticulate crest but with distinct tubulosity. The crumina is finely striate ventrally.

Dimensions.—Hinge length—sulcal height of female specimens from Hoburgen Ia: 1695 μ–1190 μ, 1635 μ–1100 μ.

Remarks.—This species differs from *L. scanensis* by its relatively much narrower syllobial loop in the male; in *L. scanensis* there is no deep lumen in the loop but only a slightly concave platform. The anterior lobe is considerably larger in *L. scanensis*; unfortunately all specimens but one in Kolmodin's material of this species are tecnomorphs, and the only female lacks the anterior part of the velum which has proved to be very different in the two species treated here and in a third species from an erratic boulder in northern Germany. The short loop on the female syllobium of *L. angustilaqueata* stands almost vertically or is inclined backwards; in *L. scanensis*, as in the material described below, there is a non-cristate body in this place, markedly inclined forwards.

Occurrence.—Hamra Beds: Hoburgen Ia, Hoburgen IIa, Hoburgen IIb.

Lophoctenella cf. *scanensis* (Kolmodin 1869)

Figs. 122 A–B.

Remarks.—As long as no specimen of *L. scanensis* has been found with the anterior part of the velum preserved or the female *Lophoctenella* species from the Hemse group have been found together with tecnomorphs, this material has to be referred to as *L.* cf. *scanensis*. It agrees with the female specimen of *L. scanensis* by the morphology of the syllobium; the damaged preadductorial lobe in *L. scanensis* must, too, have had the shape shown in Fig. 122 B, not a loop as in *L. angustilaqueata*. The material from the Hemse Beds differs from both *L. scanensis* and *L. angustilaqueata* in having a coarse striation all over the crumina; the value of this ornamentation as a differential character cannot be judged with the small number of female *Lophoctenella* specimens known hitherto. The greatest differences in this material, as compared with *L. angustila-*

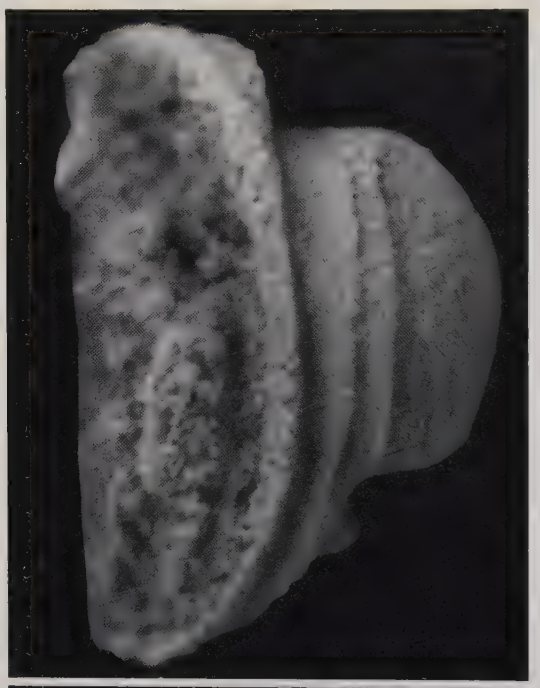


Fig. 122 A. *Lophoctenella* cf. *scanensis*. Female valve in oblique ventral view (anterior end up) showing velar edge and torus on the crumina. No. G 503. Hulte. ×50.

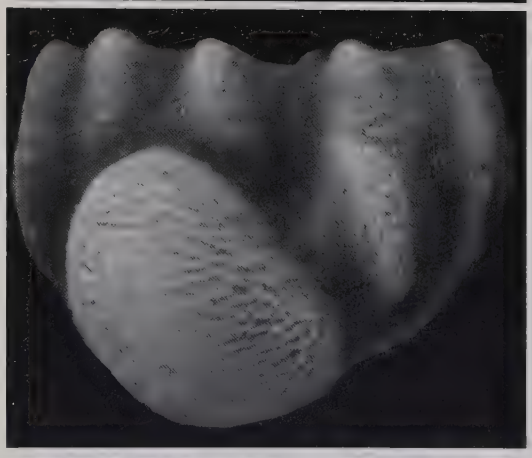


Fig. 122 B. *Lophoctenella* cf. *scanensis*. Same specimen (No. G 503) in lateral view. ×40.

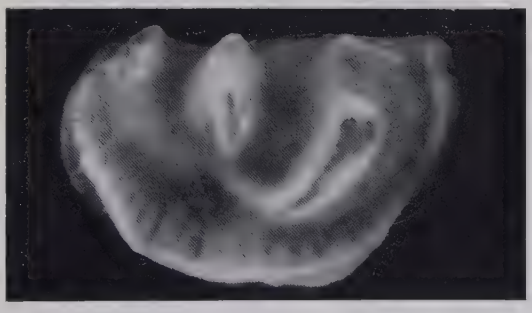


Fig. 122 C. *Cryptolopholobus semilaqueatus* n.sp., Burgsvik, Beds, Husryggen. Tecnomorph, No. G 505. ×40.

queata, concern parts of the carapace which have never been seen in *L. scanensis*, viz. the well developed anterior lobe and the anterior part of the velum which lacks the typical, well delimited comb of *L. angustilaqueata*. There is one fragmentary *Lophoctenella* tecnomorph found in the Hemse Beds, at Fie, very similar to the tecnomorphs of *L. angustilaqueata*. If this specimen is conspecific with the females, it can be definitely established that the material from the Hemse Beds represents a new species.

Occurrence.—Hemse Beds: Hulte (very rare), Botvide (very rare), Fie (only the problematic tecnomorphic specimen mentioned).

Genus *Cryptolopholobus* n.g.

Fig. 98F.

Derivation of the Name.—Greek κρυπτος, concealed, λόφος, as in the preceding genus, and Greek-Latin *lobus*, lobe, referring to the almost obsolete cristal loops in the females.

Type Species.—*Cryptolopholobus semilaqueatus* n.sp.

Species.—Only the type species.

Diagnosis.—*Amphitoxotidinae* with cristal loops on the syllobium and the predductorial lobe of the male; in the female the loops are almost completely effaced. The anterior lobe communicates with the others by a low lobal ridge. Denticulate border crest developed only anteroventrally in the male. The velar edge, but not the torus, continues across the crumina, and is slightly curved down towards the base of the crumina.

Remarks.—As in *Lophoctenella*, the sexual dimorphism has influenced considerable parts of the carapace in addition to the velar region. The ventral morphology of the crumina might seem very different from that in *Lophoctenella*, but a species of the latter genus in erratics from northern Germany shows a deflection of the velar edge very similar to that in *Cryptolopholobus*, though the torus continues along it. In addition to the material from Gotland there is also an undescribed *Cryptolopholobus* material from the Silurian of Scania.

Cryptolopholobus semilaqueatus n.sp.

Figs. 122C and 123.

Derivation of the Name.—Latin *semilaqueatus*, provided with half a loop, referring to the arrangement of the ornamentation on the syllobium.

Holotype.—A right female valve, No. G 498 (Fig. 123A and F).

Type Stratum and Type Locality.—Burgsvik Beds at Husryggen, Gotland.

Diagnosis.—As for the genus.

Description.—Anterior lobe in the male connected with the others as stated in the diagnosis. The preadductorial lobe has a small cristal loop; a larger,

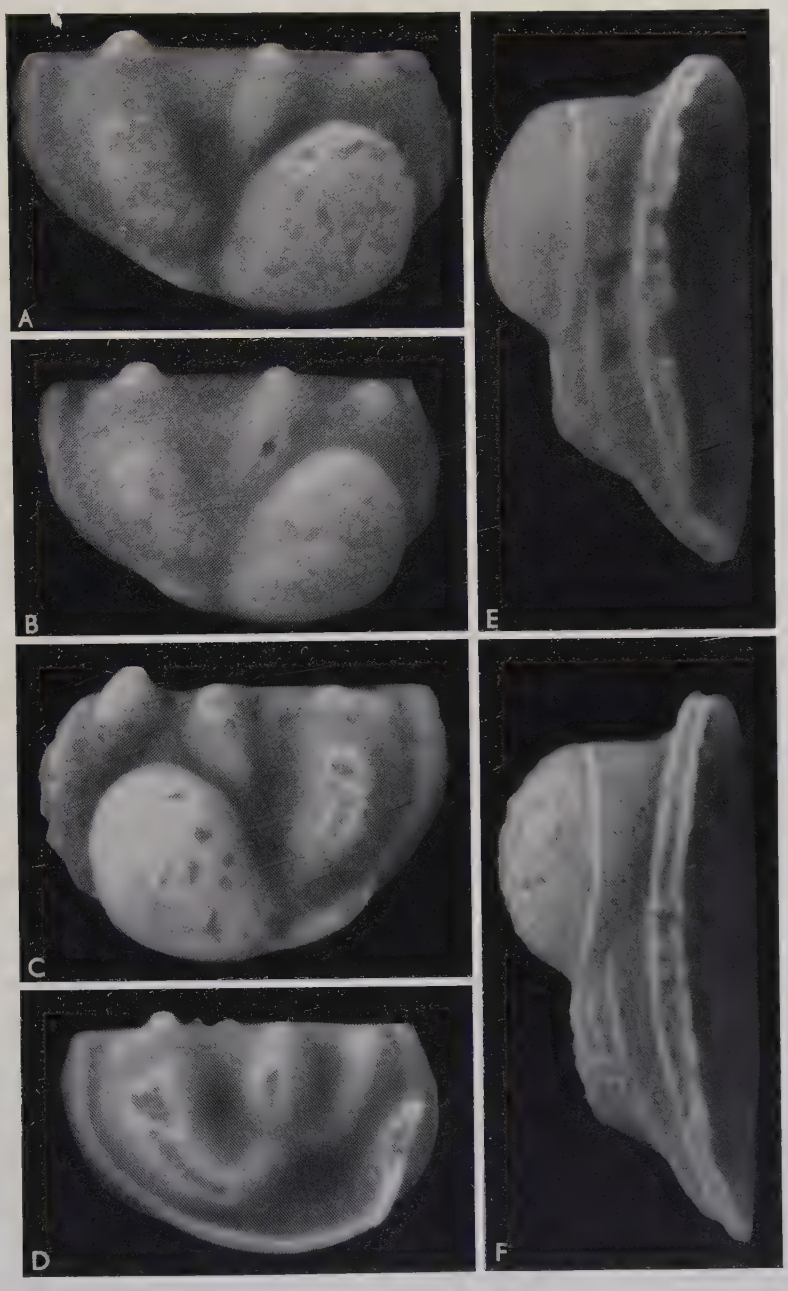


Fig. 123. *Cryptolopholobus semilaqueatus* n.sp., Burgsvik Beds, Husryggen A–D × 40, E–F × 50. A. Female valve, No. G 498 (holotype). B. Female valve, No. G 499. C. Female valve, No. G 501. D. Tecnomorph, No. G 502. E. Female valve in ventral view anterior end up. No. G 500. F. The holotype (No. G 498) in similar orientation.

dorsally characteristically truncate loop is developed over a little more than the lower two thirds of the syllobium. There is often an oblique crista across the lumen of the syllobial loop (Fig. 123 D).

In the female only the cuspidal part of the anterior lobe is left over the crumina; the lower part of the preadductorial lobe is also somewhat displaced by the inflation of the crumina. The general shape of the syllobium is as in the male. There is no cristal loop at all on the preadductorial lobe of the female, and the corresponding part of the syllobium is marked only by a structural differentiation of the carapace wall which may, in extreme cases, give an idea of the outline of a syllobial loop (Fig. 123).

In both sexes the syllobial cusp protrudes over the hingeline; this may in rare cases also be true of the cusp of the anterior lobe (Fig. 123 C).

In the male (and in the smaller tecnomorphs) the velum begins with a denticulate portion at the most anterior point of the valve; this portion passes over anteroventrally into a ventral portion with a non-denticulate border crest, and posteroventrally it gently passes over into a velar ridge; in the female this transition can be a little more marked. The tubulosity is distinct only anteroventrally in the male, in the region of the deep anteroventral depression.

The velar ridge on the crumina is described in the diagnosis. The toric structure on the postcruminal portion of the velum (Figs. 123 E–F) consists of two subparallel ridges; the outer of them is very short.

Dimensions.—Hinge length—sulcal height of female specimens from the type locality, in microns: 1330–930, 1305–860, 1290–990, 1285–840, 1240–830 (as is often the case, the height measurements are not reliable owing to varying influence of compression or distortion .

Occurrence.—Burgsvik Beds: Husryggen. Hamra Beds: Sles, Hoburgen II b.

Genus *Lauella* n. g.

Fig. 99 D.

Derivation of the Name.—Femine diminutive of a Latin adjective *Lauus*, inhabitant of the parish of Lau.

Type Species.—*Lauella uncinata* n.sp.

Species.—*Lauella uncinata* n.sp.

Lauella n.sp.

Diagnosis.—*Amphitoxotidinae* with isolated anterior lobe in the tecnomorphs. Velar edge obsolete or very vaguely traced across the crumina. A toric ridge continues from the postcruminal portion of the velum across the crumina. There is no precruminal velum. Syllobium broad, markedly set off from a triangular area near the posterior hinge corner.

Remarks.—The tecnomorph in *L. uncinata* shows a specialization unknown in other ostracodes, viz. a hooked process anteroventrally. This is probably the most characteristic feature in the genus, but as long as the tecnomorphs of the

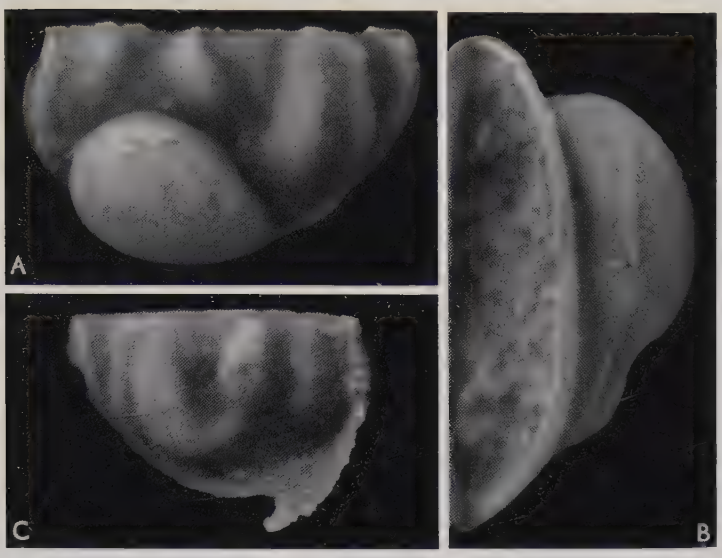


Fig. 124. *Lauella uncinata* n.sp., Eke Beds, Lau Backar. A. Female valve, No. G 506 (holotype). ×40. B. Same specimen in oblique ventral view, anterior end up. ×60. C. Tecnomorph, No. G 507. ×40.

species from the Hemse Beds are unknown it should not be added to the generic diagnosis. Probably a slight elevation at the most distal point of the obsolete or almost obsolete velar edge on the crumina is common, but the material is so small that the constancy of this feature cannot be proved.

Lauella uncinata n.sp.

Fig. 124.

Derivation of the Name.—Latin *uncinatus*, provided with a small hook, referring to the male velum.

Holotype.—A left female specimen, No. G 506 (Fig. 124A–B).

Type Stratum and Type Locality.—Eke Beds at Lau Backar, Gotland.

Diagnosis.—*Lauella* species with a ridge along the syllobium separated from its main body by a depression from its cuspidal part to the velar base. No velar edge across the crumina.

Description.—The lobes, described in the diagnoses (cf. Fig. 124), do not protrude over the hingeline. The connection between the preadductorial lobe and the syllobium is very suggestive of the zygal arch in other subfamilies (this term has been avoided in the *Amphitoxotidinae* as the connection is morphologically wider than the zygal ridge).

The velum in the female is only a short ridge or very low flange immediately behind the crumina, passing over into the low lobal ridge along the syllobium (note that *Vinculoveliger*, Figs. 127–128, has a similar arrangement). In the

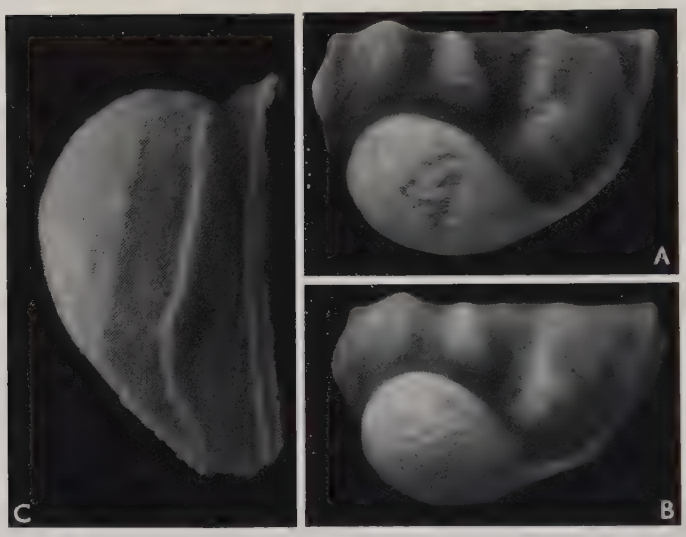


Fig. 125. *Lauella* n.sp., Hemse Beds. Hammarudden. A–B. Female valves in lateral view, Nos. G 509 and G 510. × 40. C. Female valve in ventral view, anterior end up, No. G 508. × 60.

male the velum begins at the most anterior part of the carapace, widens strongly anteroventrally but is suddenly cut down into a much narrower flange below the prenodal sulcus. The anteroventral, wider part of the velum is tubulous, and the most posterior of tubules is drawn out and bent backwards into the hook which is referred to in the specific name.

The toric ridge of the postcruminal velar portion becomes very low at the transition onto the crumina but again becomes more marked on the crumina.

There is a fine reticulation or very dense punctation on all lobes.

Dimensions.—Hinge length of the holotype 1240 μ, height over the posterior part of the adductorial sulcus 720 μ.

Remarks.—This species differs from the other, unnamed *Lauella* sp. by the absence of a bend on the crumina marking the continuation of the velum, and by the very low junction of the ridge along the syllobium and the velar flange.

Occurrence.—Eke Beds: Lau Backar (one female and one tecnomorph in a very large quantity of marl).

Lauella n.sp.

Fig. 125.

Remarks.—This species, very rarely represented in the ostracode fauna between two of the limestone layers in the Hemse Beds at Hammarudden, shows some primitive features of the genus *Lauella*. The velar edge is not obsolete on the crumina but continues across it, forming a somewhat wider elevation at its most distal point—a similar elevation can possibly be discerned also in *L. uncinata*. The toric ridge is very high, bent, but not interrupted, at

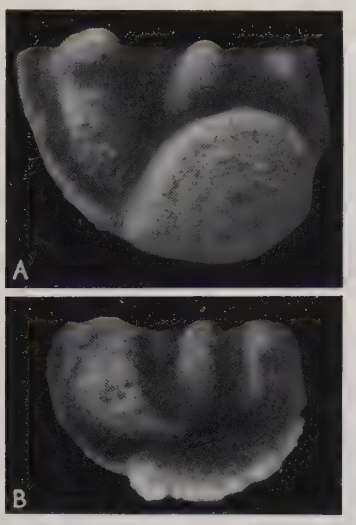


Fig. 126. *Grogarnia atlantica* n.sp., Hemse Beds, Hammarudden. ×40. A. Female valve, No. G 511 (holotype). B. Tecnomorph, No. G 512.

the transition onto the crumina. Another character which might be primitive is the very high junction of the ridge on the posterior part of the syllobium with the velum; thus there is no longitudinal depression on the syllobium. The anterior lobe protrudes slightly over the hingeline. No tecnomorph is known, and a species of this genus can hardly be described from a material without tecnomorphs.

Genus *Grogarnia* n.g.

Derivation of the Name.—Latin *Grogarnius*, inhabitant of the region of Grogarns and Grogarnsberget in the parish of Östergarn (no representative of the genus, however, is found at the locality with the code name of Grogarns in this paper).

Type Species.—*Grogarnia atlantica* n.sp.

Species.—Only the type species.

Diagnosis.—*Amphitoxotidinae* with an isolated anterior lobe, a broad syllobium and a very large crumina. No velar edge or torus across the crumina. Wide velum in the tecnomorphs, suddenly restricted slightly behind a line along the posterior limit of the adductorial sulcus.

Grogarnia atlantica n.sp.

Fig. 126.

Derivation of the Name.—Latin *Atlanticus*, like Atlas (in carrying a large globe), referring to the relative size of the crumina.

Holotype.—A right female valve, No. G 511 (Fig. 126A).

Type Stratum and Type Locality.—Hemse Beds at Hammarudden, Gotland.

Diagnosis.—As for the genus.

Description.—The cuspidal part of the syllobium can be isolated by a shallow depression from the main body of the syllobium; the connection between the syllobium and the preadductorial lobe is very low.

In the female the velum in front of and behind the crumina is a narrow flange. The crumina is very large, suppressing almost half of the anterior and preadductorial lobes. There is no velar edge, nor any torus, seen on the crumina in normal conditions; if the crumina is turned in strongly inclined light it can be observed that there is a very slight faceting of the crumina resulting in a bend in the continuation of the velum; at the most distal point of this bend there is an almost indiscernible, wider elevation as is possibly also the case in *Lauella uncinata*.

In the male the ventral and anteroventral parts of the velum are wide and tubulous, limited as stated in the diagnosis. The wide part of the male velum almost exactly coincides with that occupied by the crumina in the female; only just below the anterior cardinal corner is there a more far-reaching restriction of the female velum.

The lobal ornamentation is a very fine reticulation, with a tendency towards verrucosity on the posteroventral part of the syllobium. Laterally, the crumina is reticulo-striate, on its ventral side the reticulation becomes more regular.

Dimensions.—Hinge length of the holotype 1130 μ, sulcal height 705 μ.

Occurrence.—Hemse Beds: Hammarudden.

Genus *Vinculoveliger* n.g.

Figs. 99B and 127.

Derivation of the Name.—Latin *vinculum*, bond, chain, *velum*, and *-ger*, bearer or carrier of, referring to the conditions along the base of the (broken) velum.

Type Species.—*Vinculoveliger catenulatus* n.sp.

Species.—Only the type species.

Diagnosis.—Large, completely lobate *Amphitoxotidinae* with a wide, restricted velum with a basal crest in the male and a low velar ridge in the female.

Vinculoveliger catenulatus n.sp.

Fig. 128.

Derivation of the Name.—Latin *catenulatus*, provided with a chain.

Holotype.—A left female specimen, No. G 513 (Fig. 128A).

Type Stratum and Type Locality.—Hemse Beds at Medbys, Gotland.

Diagnosis.—As for the genus.

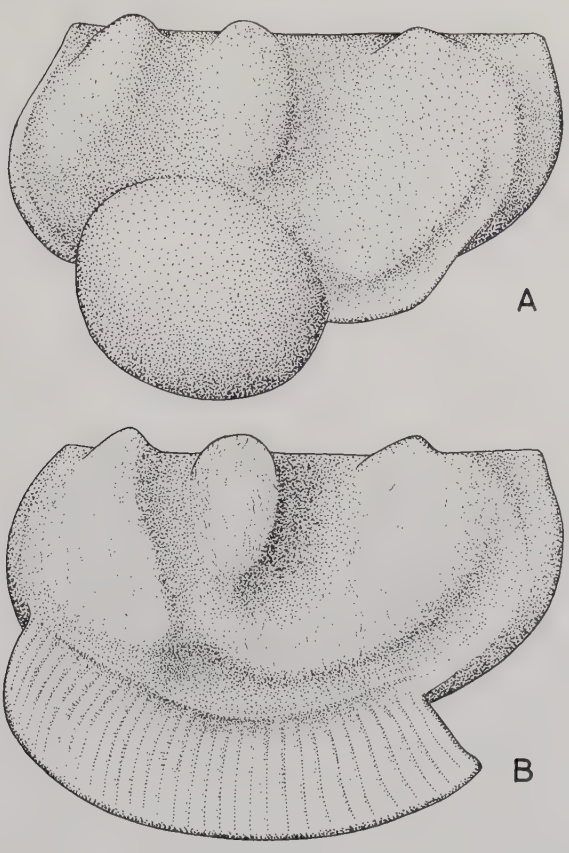
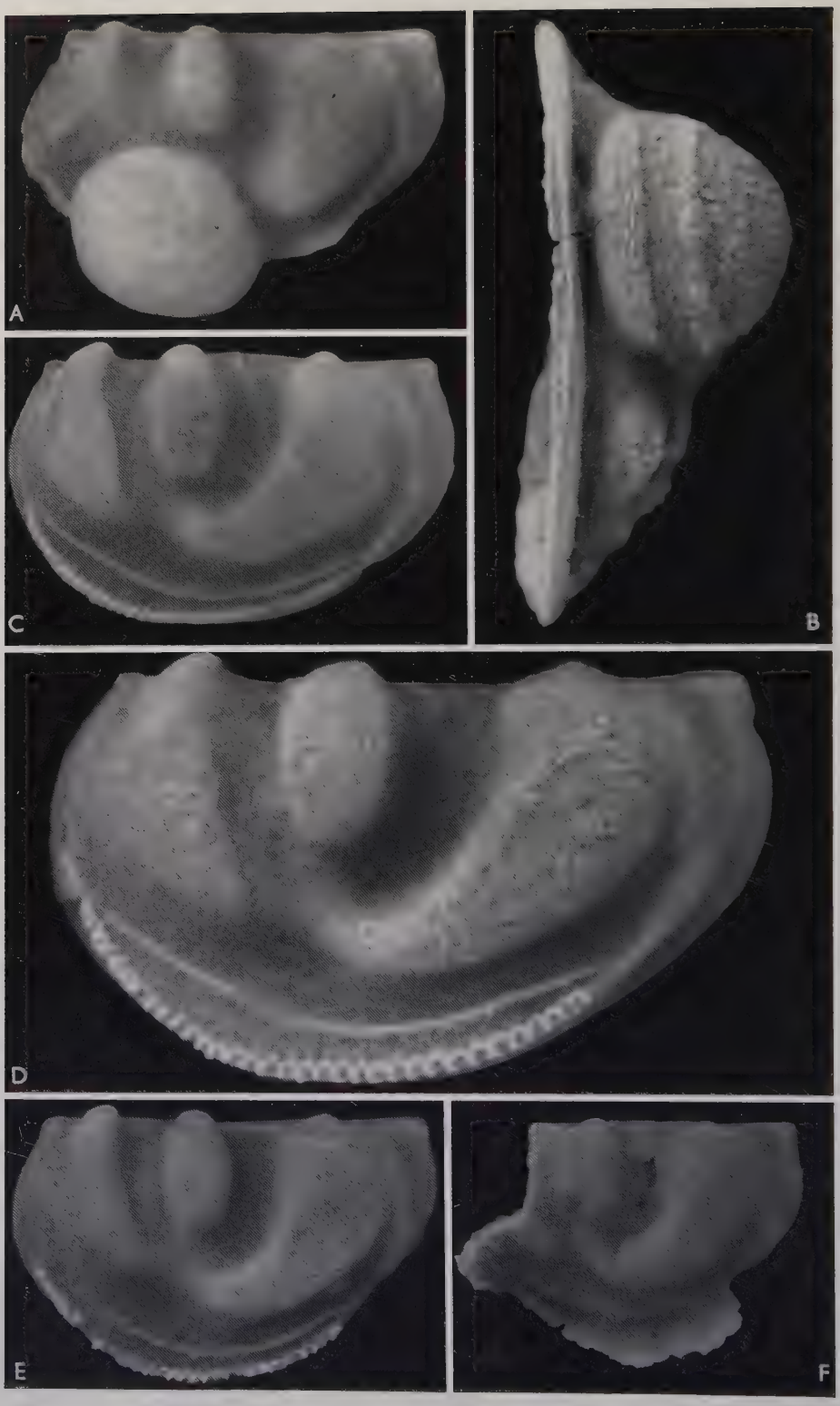


Fig. 127. *Vinculoveliger* n.g. Reconstructive drawing based on *Vinculoveliger catenulatus* n.sp. Ornamentation slightly simplified. × 35. A. Female. B. Male.

Description.—Lobes almost completely isolated from each other; only the syllobium has a very low connection towards the lower end of the prenodal sulcus so that the adductorial sulcus becomes isolated from the anteroventral depression. The lateral surfaces of the lobes are flattened; this becomes particularly evident in the preadductorial lobe of the tecnomorphs (Fig. 128D). Anterior lobe and syllobium broad; the syllobium has the same tendency as in *Lauella* to develop a ridge along the posterior part of the syllobium which passes over into the velar ridge. All lobes protrude over the hingeline.

The velum is very different in the two dimorphs. Anteriorly and posteriorly the velum is a low ridge even in the male, but a little below the most anterior part of the valve it widens into a frill continuing along all the ventral part of the valve. The frill is very wide but also very thin, though only occasionally parts of its edge are intact. Typically this part of the velum is broken off along a distinct line in the continuation of the velar flange behind the restriction,


A
B
C
D
E
F

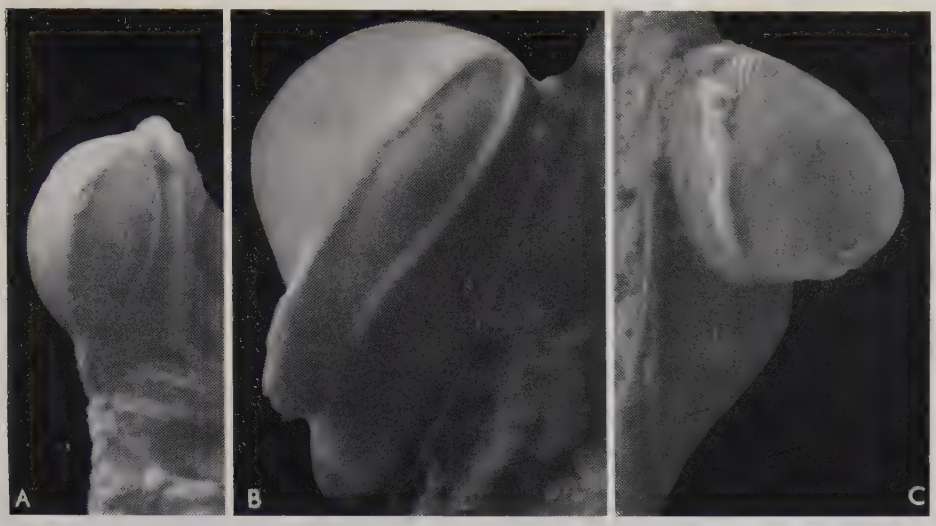


Fig. 129. Ventral morphology of the crumina in some *Amphitoxotidinae* from the Silurian of the Baltic area, found in erratics in North Germany. × 40. A. *Berolinella steusloffi* (KRAUSE). B. *Berolinella* n.sp. C. Specimen figured by KUMMEROW 1943, Pl. II, fig. 7 as *Beyrichia alata* n. nom. (unrevised). Cf. *Beyrichia latispinosa* PŘIBYL (PŘIBYL 1951, Fig. 1). All specimens in the Palaeontological Museum of the Humboldt University, Berlin.

and the walls of the tubules form a very decorative chain of small rings. Subparallel to this chain and of the same length is the basal crest. The anterior limitation of the wide part of the velum is probably gently rounded anteriorly; posteriorly it is abruptly cut down along a tubule.

In the female nothing is left of the wide part of the velum or the basal crest along it. The low velar ridge has a higher, flange-like portion behind the crumina. The crumina is almost globular, relatively small, and incorporating the lower parts of the anterior and preadductorial lobes. The crumina has ventrally a subequatorial ridge, corresponding to the velum, and a basal, broad, striate swelling which is probably of toric origin (Fig. 128 B).

The surfaces of the lobes have a characteristic reticulo-striation which is especially distinct in the male. The female is almost smooth; the same is true for the crumina, except for its toric region and a fine striation in the zone between this region and the velar edge.

DIMENSIONS.—Hinge length—sulcal height of female specimens from Medbys: 1865 μ–1130 μ, 1816 μ–1220 μ, 1715 μ–1080 μ.

OCCURRENCE.—Hemse Beds: Medbys, Tjängdarve, Linde, Amlings.

Fig. 128 (opposite page). *Vinculoveliger catenulatus* n.sp., Hemse Beds, Medbys. D × 50, B × 40, others × 30. A. Female valve, No. G 513 (holotype). B. Female valve, No. G 514. C. Tecnomorphic valve, No. G 515. D. Tecnomorphic valve, No. G 516, showing details in the ornamentation. E. Tecnomorphic valve, No. G 517. F. Tecnomorphic valve, No. G 518, with preserved parts of the velum.

Genus *Berolinella* n. g.

Figs. 129A–B.

Derivation of the Name.—Feminine diminutive of Latin *Berolinus*, associated with *Berolinum*, the city of Berlin.

Type Species.—*Beyrichia Steusloffi* Krause 1891.

Species.—*Beyrichia Steusloffi* Krause 1891.

Berolinella n.sp.

Diagnosis.—*Amphitoxotidinae* having a basal crest along a wide, tubulous velum in both sexes. Sulcus or sulci communicating with the narrow depression above the basal crest. The velar edge continues more or less uninfluenced across the crumina; the torus forms a sharp basal ridge similar to the outer basal crest, but in contrast to this crest it continues across the crumina.

Remarks.—*Beyrichia steusloffi* has been mentioned in faunal lists from Gotland (cf. p. 44), but in this connection it is mainly the illustrative cruminal morphology that motivates the anticipation of a forthcoming revision of the erratic material of this genus (the specimens figured by Krause 1891, Pl. XXXII, figs. 8 and 9 are preserved). *Berolinella steusloffi* is the amphitoxotidine in which the least incomplete inflation of the velum has taken place so that there are even tubules left in the part of the velum which continues across the crumina (Fig. 129A, cf. Kesling 1956a). This species has two very similar sulci, the prenodal and the adductorial, extending from the hingeline down to the base of of the velum. In *Berolinella* n.sp., however, only the lower part of the adductorial sulcus is distinct, and its crumina occupies the velar fold more completely. There is only a velar ridge across the crumina, and at its most distal point on the crumina there is a small constriction, at the bottom of which there is a very fine pit or hole of unknown depth (Fig. 129B), as remains of the abandoned dolonoid closing apparatus.

Recently Kesling (1956a) referred *Beyrichia steusloffi* to *Dibolbina* (cf. Ulrich & Bassler 1923) and made a reconstruction of the species showing it with an entire velum. However, the genus *Berolinella* differs from *Dibolbina* in having posterior restriction of the velum of the same kind as *Vinculoveliger* and *Atterdagia*, in lacking a characteristic ridge of cristal appearance present on the syllobium of *Dibolbina* and in following up trends in the sulcal development which do not lead to the formation of a thinly reniform sulcal pit bent around a small preadductorial node as in *Dibolbina*.

Genus *Atterdagia* n. g.

Figs. 99H and 130.

Derivation of the Name.—From a Latin adjective *Atterdagius*, associated with Valdemar Atterdag, King of Denmark and conqueror of Visby and Gotland in 1361.

Type Species.—*Atterdagia paucilobata* n.sp.

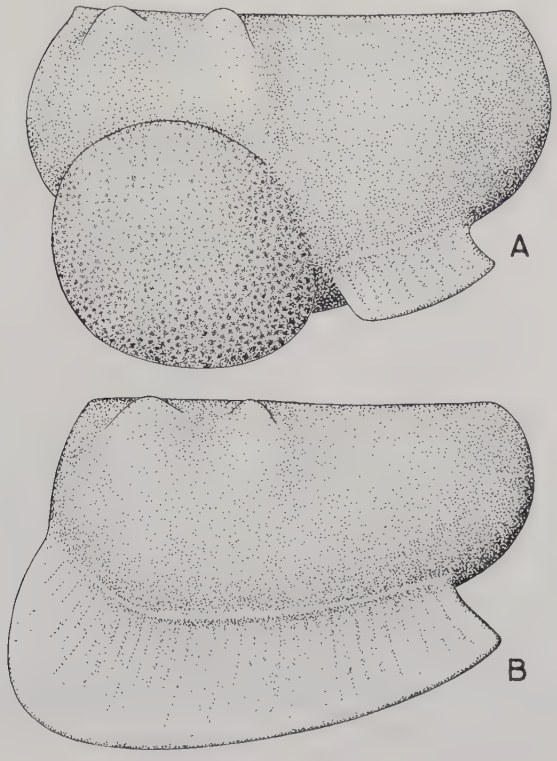


Fig. 130. *Atterdagia* n.g. Reconstruction based on material of *Atterdagia* paucilobata n.sp. There is some uncertainty as to the remains of the lobation in the male. ×45. A. Female. B. Male.

Species.—Only the type species.

Diagnosis.—*Amphitoxotidinae* with a basal crest along the velum in both sexes. Lobation, if discernible at all, consisting only of the most dorsal parts of the anterior and preadductorial lobes. Velum in the female developed only as a postcruminal wing, separated from the crumina.

Atterdagia paucilobata n.sp.

Fig. 131.

Derivation of the Name.—Latin *paucilobatus*, provided with few lobal features.

Holotype.—A left female valve, No. G 519 (Fig. 131 A).

Type Stratum and Type Locality.—Hemse Beds at Tjängdarve, Gotland.

Diagnosis.—As for the genus.

Description.—The only lobal features are mentioned in the diagnosis; there is a very shallow depression in the region of the adductorial sulcus. However, it is uncertain whether there are any lobes marked at all in the tecnomorphs.

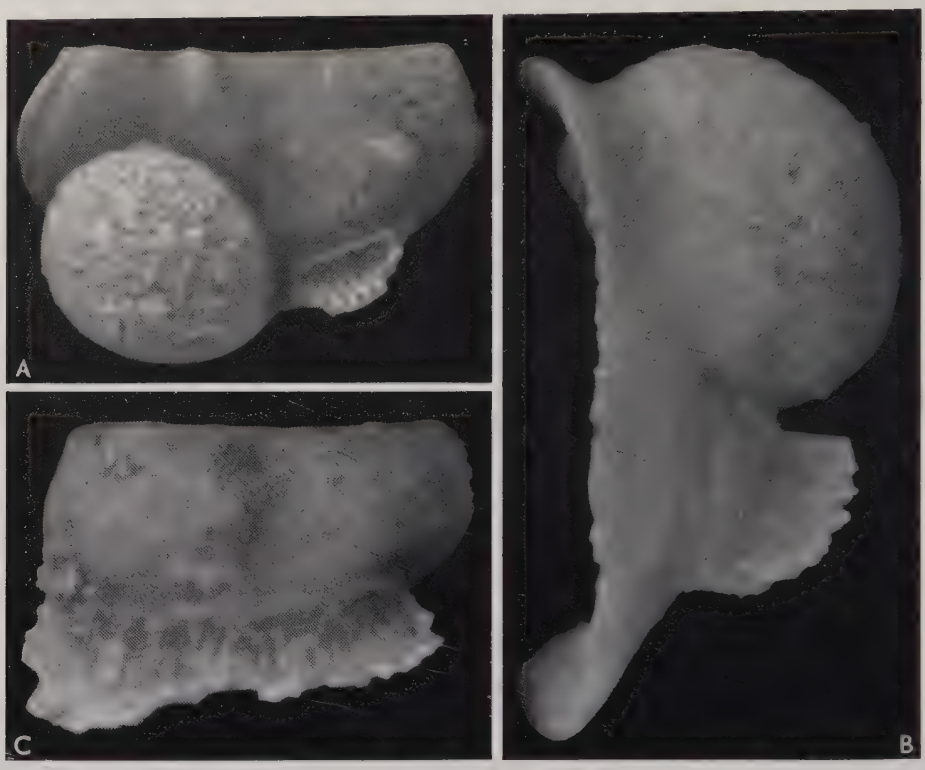


Fig. 131. *Atterdagia paucilobata* n.sp., Hemse Beds, A from Tjängdarve, B–C from Hulte. A. Female valve, No. G 519 (holotype) ×40. B. Female valve in ventral view, anterior end up, No. G 520. ×50. C. Tecnomorph, No. G 521. ×40.

The very broad tecnomorphic velum begins at the most anterior part of the valve and is abruptly restricted posteroventrally without any distinct continuation in a velar ridge. The only velar feature in the female, except those included in the crumina, is the tubulous wing referred to in the diagnosis. There is a basal crest along all frill-like parts of the velum in both sexes. There is a basal toric ridge even on the small female velar wing, but neither the velar edge nor the torus can be traced across the crumina.

The sides of the valves are unornamented. All sides of the crumina are finely reticulate.

Dimensions.—Hinge length of the holotype 1310 μ, sulcal height 925 μ.

Remarks.—The parallel development of the outer basal crest and the basal toric crest in this and related genera—as well as the distal outer ornamental ridge and the distal toric ridge in several *Craspedobolbininae*—is suggestive of a genetic relationship between these two structures, the outer of which is often missing. The tubules are in both cases developed both distally and basally of the structures in question. It is known already that an analysis of the ventral

morphology of the male would make the picture presented here of the beyrichiid adventral morphology much more detailed but the technical work necessary for such a consistent study would have taken a year without contributing essentially to the main theme of this paper.

Occurrence.—Hemse Beds: Tjängdarve, Hulte, Fie (very rare).

Genus *Macrypsilon* n.g.

Derivation of the Name.—Greek μακρός, large, and ὐ ψιλόν, the letter *y*, referring to the arrangement of the sulci.

Type Species.—*Beyrichia Salteriana* Jones 1855.

Species.—Only the type species.

Diagnosis.—*Amphitoxotidinae* with very broad lobes. In the tecnomorphs the narrow sulci are united below the preadductorial lobe into an equally narrow sulcus separating the syllobium and the anterior lobe. Crumina very large. Velum forming a narrow flange from the anterior to the posterior hinge corner, but the tubulosity within it is discernible. All lobes finely reticulate.

Remarks.—The lectotype of *Macrypsilon salterianum* is refigured here (Fig. 2 D), and both dimorphs have been figured by Kesling & Rogers 1957 (Pl. 128, figs. 14–17). This genus is an important constituent of the erratic Upper Ludlovian faunas and is included here to show another, isolated branch of amphitoxotidine development.

Incertae subfamiliae, n.g. n.sp.

Fig. 132.

Remarks.—This species, known only from six female specimens, is too interesting from the morphological point of view to be neglected owing to the lack of sufficient material. It is extremely small (hinge length—sulcal height of female specimens from Sles: 720 μ–485 μ, 690 μ–440 μ, 665 μ–415 μ), has a complete set of lobes as in primitive beyrichiids and a relatively large crumina. It is an amphitoxotidine or a beyrichiine but differs from most *Amphitoxotidinae* by having a well-developed calcarine spine and from most *Beyrichiinae* by having a well developed velar flange behind the crumina. However, it might well be related to the small calcarate *Beyrichia* (*Simplicibeyrichia*) species. It is known only from the Hamra Beds of Sles and Lunde.

Subfamily *Zygobolbinae* Ulrich & Bassler 1923

Type Genus.—*Zygobolba* Ulrich & Bassler 1923

Genera.—*Zygobolba* Ulrich & Bassler 1923
Zygobolbina Ulrich & Bassler 1923
Plethobolbina Ulrich & Bassler 1923

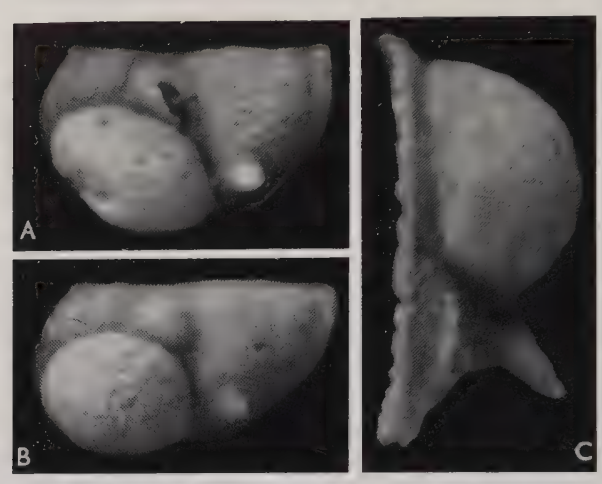


Fig. 132. *Incertae subfamiliae*, n.g., n.sp. Hamra Beds, Sles. Female valves. A. No. G 522, ×50. B. No. G 524, ×50. C. No. G 523, ventral view, anterior end up, ×75.

Zygosella Ulrich & Bassler 1923
Mastigobolbina Ulrich & Bassler 1923
Bonnemaia Ulrich & Bassler 1923
Slependia n.g.
Noviportia n.g.

Diagnosis.—*Beyrichiidae* with a flange- or ridge-like velum. Anteroventral crumina; the dolonoid scar consists of a fissure or fold breaking through the margin.

Remarks.—The dolonoid scar has been observed only in *Zygobolba*, *Noviportia*, and—with some uncertainty—in *Slependia*. The other genera have been included only on the evidence of characters in their lateral lobal and cruminal morphology.

The nature of the dolonoid scar in this subfamily and the procedure leading to its formation are not known with any degree of certainty. Possibly the dolonoid stage was represented only by a plication which implied the retraction of the marginal part of the fold so that the scar cuts through the margin.

In most of these genera the anterior lobe is very inconsiderable—or even obsolete—and the prenodal sulcus is very narrow. The adductorial sulcus is very broad and the syllobium relatively narrow. A typical feature in this family is the ridge present in many genera across the preadductorial node and round the zygal region, extending onto the syllobial cusp. Sometimes, as in *Zygobolba* and *Mastigobolbina*, it is very suggestive of a widened zygal crista; in *Mastigobolbina* the lower part of this primarily U-shaped ridge is drawn backwards onto the syllobium. This ridge sometimes dominates the lobation totally, as in *Zygobolbina*; in other cases, as in *Bonnemaia* and *Plethobolbina* there are two lobal complexes—the anterior of them consisting of the preadductorial and anterior lobes—widely connected below the adductorial sulcus. The velum is

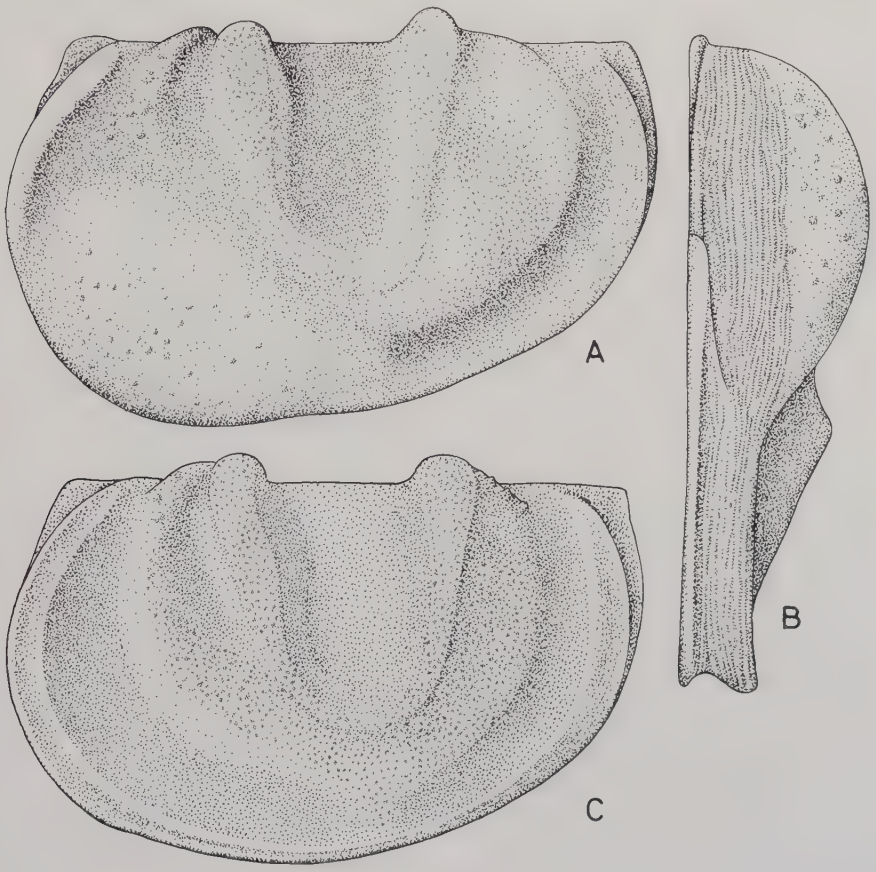


Fig. 133. *Zygobolba* Ulrich & Bassler 1923. Reconstructive drawing of the type species, *Zygobolba decora* (Billings 1866). × 30. A. Female. B. Female, ventral view, anterior end up. C. Male.

invariably flange- or ridgelike along all the non-dorsal part of the outline. The crumina generally occupies the anteroventral part of the velum and adjoining parts of the carapace wall, but sometimes, as in *Zygobolba prolixa* and *Zygobolbina conradi*, it tends to be displaced onto the carapace wall in the place of the anterior lobe. It is unknown whether these forms can also be expected to have a dolonoid scar as categorically stated in the present diagnosis.

Occurrence.—Silurian of North America and Europe. The European material comprises only the two genera *Noviportia* and *Slependia* which form a group with a lobal development different from that in the greater part of the American genera.

Zygobolba Ulrich & Bassler 1923

Figs. 133–136.

Remarks.—Material of the type species. *Zygobolba decora* (Billings) from the Jupiter formation of Anticosti Island has been examined and is figured here.

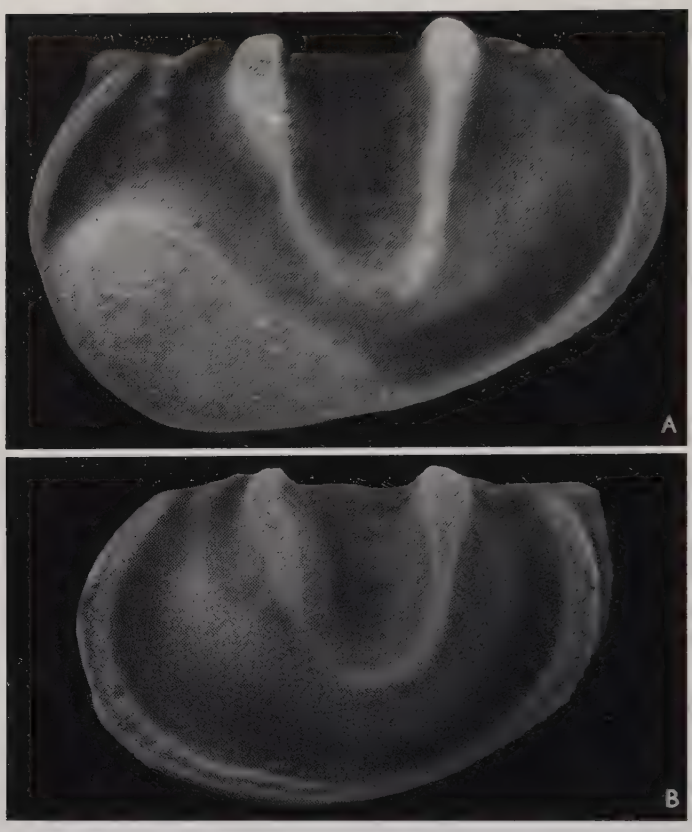


Fig. 134. *Zygobolba decora* (BILLINGS 1866) from the Jupiter River Formation, East Jupiter Cliff, Anticosti, Quebec, Canada. ×30. A. Female, No. NA 74. B. Tecnomorph, No. NA 75.

Though a complete redescription seems unnecessary for the moment, some remarks as to its morphology should be added here. An analysis of its lobal morphology and the description of the ventral morphology of the crumina tie this genus and the entire subfamily closer to the other beyrichiid subfamilies than has been the case hitherto.

The anterior lobe begins immediately in front of the ridge on the preadductorial node and is ventrally fused with this ridge and the anterior part of the syllobium. Below the adductorial sulcus the depression along the base of the velar flange in the male is interrupted by a low connection between the lobes and the velar flange. The prenodal sulcus is a low, not very marked, short depression. Already in this genus the U-shaped ridge is the most dominating feature of the valve, but it does not completely conceal the preadductorial node across which it passes, and there is still much syllobial space behind its other branch. The adductorial sulcus, enclosed by the ridge, is very broad. The

Fig. 135. *Zygobolba decora* (Billings 1866), same locality as Fig. 134. Right female valve in oblique ventral view, anterior end up. No. NA 76. ×40.

In this genus the "scar" left across the marginal structure after the cruminal metamorphosis is probably the consequence of a simpler plication than in *Noviportia*. It must be stressed that the larger number of known zygobolbine genera is unrevised, and that all traces of the dolonoid plication may have been eliminated already within the subfamily, with a crumina of the beyrichiine type as a result. As defined by the present diagnosis, the subfamily covers two rather different groups of genera, an American one with pronounced lobation and reticulate surface and a mainly European one with strongly reduced lobation and granulose surface.

ridge and the velum are characteristically flattened as seen in lateral view (Fig. 134).

In ventral view (Figs. 135 and 136) *Zygobolba* has a more familiar beyrichiid appearance. There is a flange-like velum without a torus and an equally flange- or ridge-like marginal structure. The crumina is striate ventrally in the same manner as in the *Beyrichiinae* but with much less branching of the ridges between the striae, as in *Noviportia* described below or in *Slependia armata* (= *Craspedobolbina armata*, cf. Kesling & Rogers 1957, Pl. 129, figs. 2 and 6). It may also be seen that the closing procedure of the crumina has broken through the marginal structure and the margin near the posterior end of the crumina in a manner similar to that in *Noviportia* (Figs. 137 B and 138 B).

The zygobolbine ornamentation, as exhibited by *Zygobolba*, is a fine reticulation, locally tending towards punctation, covering all prominent parts of the lobes, including the cristoid U-shaped ridge, and the flattened area along the

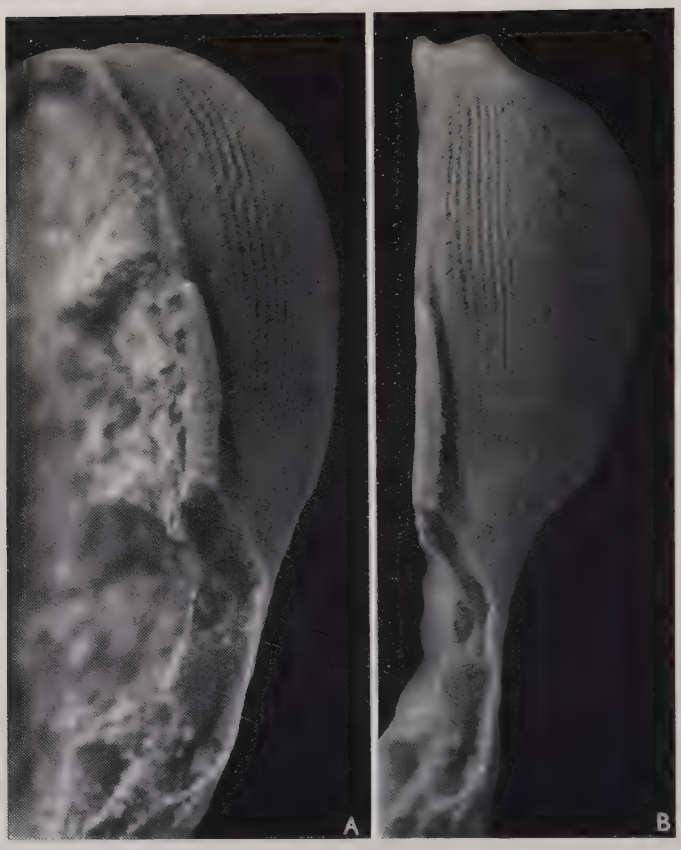


Fig. 136. *Zygobolba decora* (Billings 1866), same specimen as Fig. 134 A (No. NA 74). Left female valve in oblique ventral (A) and ventral (B) views. × 40.

non-cruminal part of the velar edge. The cuspidal part of the anterior lobe and the lateral side of the crumina are slightly verrucose. The velum locally tends to become reticulo-striate, and its inner ventral side is almost completely striate. The finger-pattern striation of the crumina has already been referred to above.

Genus *Slependia* n. g.

Cf. Kesling & Rogers 1957, Pl. 129, figs. 1–7, and
Kesling 1957b, Pl. VI, figs. 1–2 (not 3).

Derivation of the Name.—From Latin *Slependius*, inhabitant of Slependen, Asker, Norway, the type locality of the type species.

Type Species.—*Craspedobolbina armata* Henningsmoen 1954.

Species.—Only the type species.

Diagnosis.—*Zygobolbinae* with a narrow adductorial sulcus behind a preadductorial node which is fused with the anterior lobe into a lobal complex.

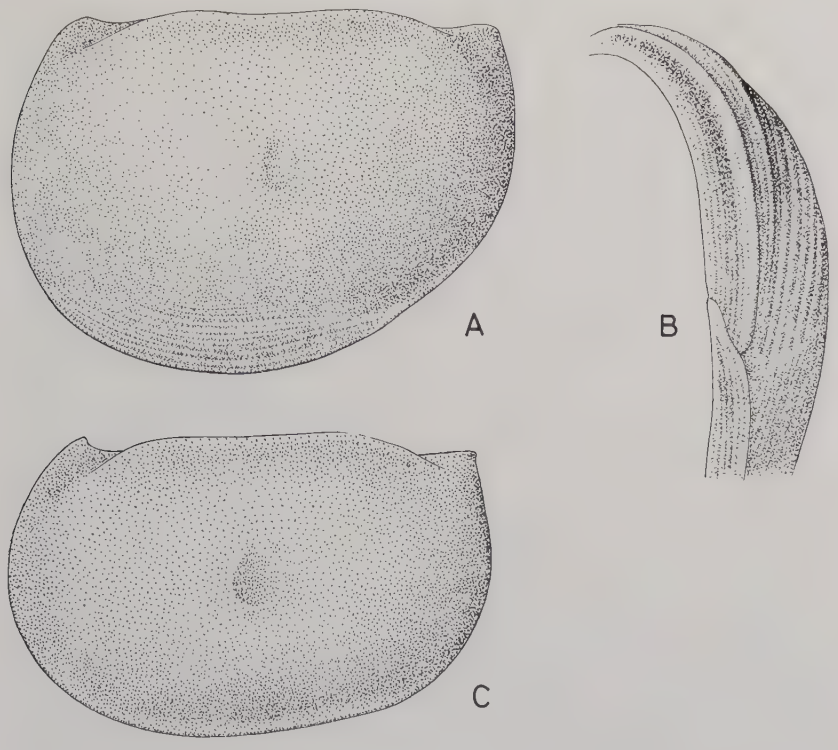


Fig. 137. *Noviportia* n.g. Drawings based on *Noviportia simpliciuscula* n.sp. × 45. A. Female. B. Ventral morphology of the crumina, anterior end up. C. Male. Note the sex ratio, 50:50. Estimated average size also indicated for moult stages 2 and 3.

Crumina with a spur, inflating the anteroventral part of the velar flange and adjoining parts of the valve.

Remarks.—The revision of *Craspedobolbina* in this paper has left the morphologically and systematically important species *Craspedobolbina armata* Henningsmoen without a generic name. This species shows a lobation which is easily derived from the primitive beyrichiid lobation and has a spur in the place where the calcarine spine of the *Beyrichiinae* is situated; in other respects, as in those parts of the cruminal morphology which can be observed in existing figures, it agrees in great detail with especially *Noviportia* but also with *Zygobolba*.

The species *Craspedobolbina expansinodata* Henningsmoen, *C. dorsoplicata* Henningsmoen, and *C. primitiva* (Verworn) (cf. Henningsmoen 1954) cannot follow *C. armata* into this new genus (cf. under *Bingeria*, p. 349).

Genus *Noviportia* n.g.

Fig. 137.

Derivation of the Name.—From Latin *novus*, new (Sw. *ny*) and *portus*, harbour (Sw. *hamn*) alluding to the fossil locality of Nyhamn, Gotland (cf. p. 46).

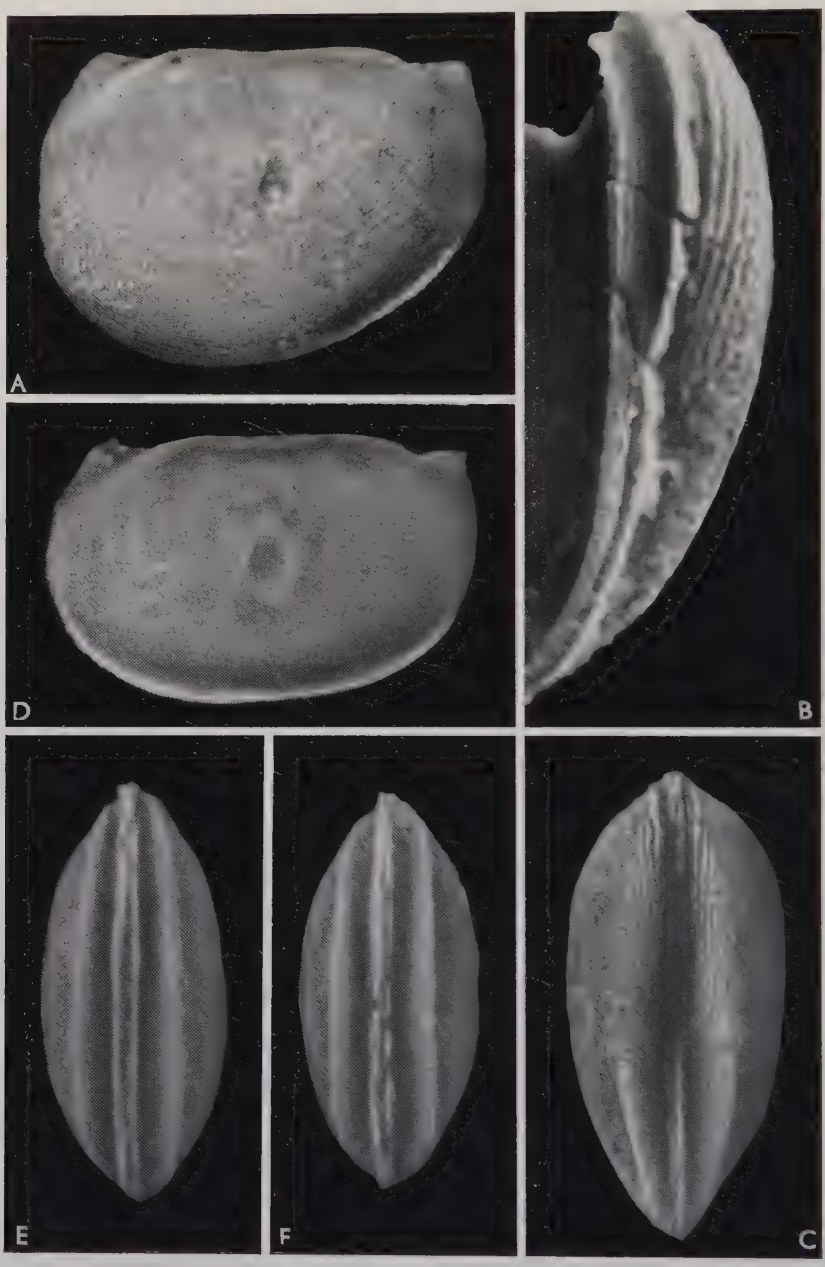


Fig. 138. *Noviportia simpliciuscula* n.sp., Lower Visby Beds. A from the Nyhamn well; B, D, and E from Nyhamn; C and F from Gustavsvik. B ×75, others ×40. A. Female carapace, No. G 525 (holotype). B. Female carapace, ventral view (anterior end up), No. G 526. C. Female carapace, ventral view, No. G 530. D. Male, No. G 527. E–F. Tecnomorphic carapaces in ventral view, Nos. G 528 and 529.

TYPE SPECIES.—*Noviportia simpliciuscula* n.sp.

SPECIES.—Only the type species.

DIAGNOSIS.—Non-sulcate *Zygobolbinae* with an adductorial spot, a high dorsal plica, and a very narrow velum.

Noviportia simpliciuscula n.sp.

Figs. 138 and 139.

DERIVATION OF THE NAME.—Diminutive comparative of Latin *simplex*, simple, referring to the lobation of the species.

HOLOTYPE.—A female carapace, No. G 525 (Fig. 138A).

TYPE STRATUM AND TYPE LOCALITY.—Lower Visby Beds at Nyhamn, Well, Gotland.

DIAGNOSIS.—As for the genus.

DESCRIPTION.—The cuspidal part of the anterior lobal complex and the syllobium are joined in a biundulate dorsal plica. The adductorial spot is oval, pointing upwards; sometimes it even curves around the site of a small, obsolete preadductorial node. There are no other traces of a beyrichiid lobation.

The velum is, along all its length, a ridge or a very low flange. The vertical marginal structures are wide flanges without traces of tubulosity.

The crumina is an anterior swelling of the velum and of adjoining parts of the carapace walls, without any marked delimitation from other parts of the carapace. At the posterior end of the crumina the dolonoid scar (Fig. 138B) cuts through the margin and the marginal structures.

The ornamentation of the lobal parts of the valves is a granulosity; the granules locally become arranged into rows, and anteroventrally in both sexes there is a perfect striation. In the female there is a coarser striation ventrally on the crumina, and the shelf outside the marginal structures is also striate. The inner, ventral side of the velum is finely striate.

In the right valve the straight ventral hinge groove dominates; the dorsal groove tapers from the hinge corners and becomes obsolete not far from them. In the left valve there are corresponding ridges. At the hinge corners there are processes similar to the acroidal processes in the *Craspedobolbininae*.

DIMENSIONS.—Total length of the adult female 1430 μ–1550 μ; height across the adductorial region 840 μ–1070 μ. Corresponding dimensions in the male 1390 μ–1600 μ and 790 μ–1030 μ. See also Fig. 147.

REMARKS.—Two tecnomorphic specimens, possibly only differing from *N. simpliciuscula* by a somewhat wider velar flange, occur in the material of *Apatobolbina* from the Jupiter River Formation of Anticosti Island investigated here. Furthermore, one of the specimens figured by HENNINGSMOEN (1954, Pl. 5, figs. 1–3) as tecnomorphs of *Craspedobolbina dorsoplicata* is not conspecific

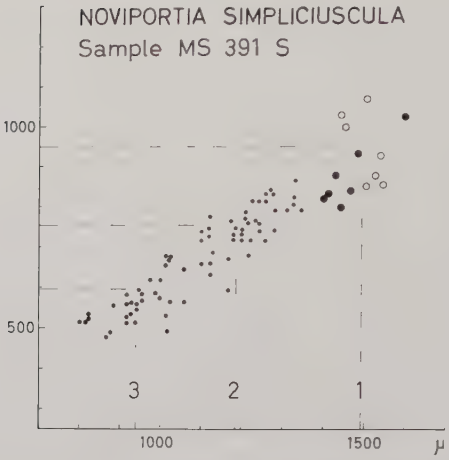


Fig. 139. Size dispersion in the late ontogeny of *Noviportia simpliciuscula* n.sp. from Nyhamn. Sulcal height along the ordinate, total length (not hinge length as in all other length measurements in this paper) along the abscissa. Female specimens set down as circlets, males as larger dots, tecnomorphs as small dots.

with the other, sulcate specimens figured but is probably a *Noviportia* species with a non-undulate dorsal plica.

Occurrence.—Lower Visby Beds: Nyhamn, Nyhamn Well, Gustavsvik, Buske.

Subfamily *Beyrichiinae* Matthew 1886

Fig. 140.

Type Genus.—*Beyrichia* M'Coy 1846.

Genera.—*Eobeyrichia* Henningsmoen 1954
Beyrichia M'Coy 1846
Neobeyrichia Henningsmoen 1954
Calcaribeyrichia n.g.
Plicibeyrichia n.g.
Gannibeyrichia n.g.
Navibeyrichia n.g.
? *Bingeria* n.g.
? *Lophokloedenia* Swartz & Whitmore 1956
? *Zygobeyrichia* Ulrich 1916
? *Welleriopsis* Swartz & Whitmore 1956

Diagnosis.—*Beyrichiidae* forming the crumina by direct occupation of the anteroventral part of the shallow velar fold and adjoining parts of the carapace wall, without a dolonoid scar but often with a striate area on the ventral part of the crumina. Remains of the zygal ridge, if present at all, obviously influenced but sometimes only slightly displaced by the inflation of the crumina.

Remarks.—As discussed by Martinsson (1960c, p. 16; cf. p. 32 of this

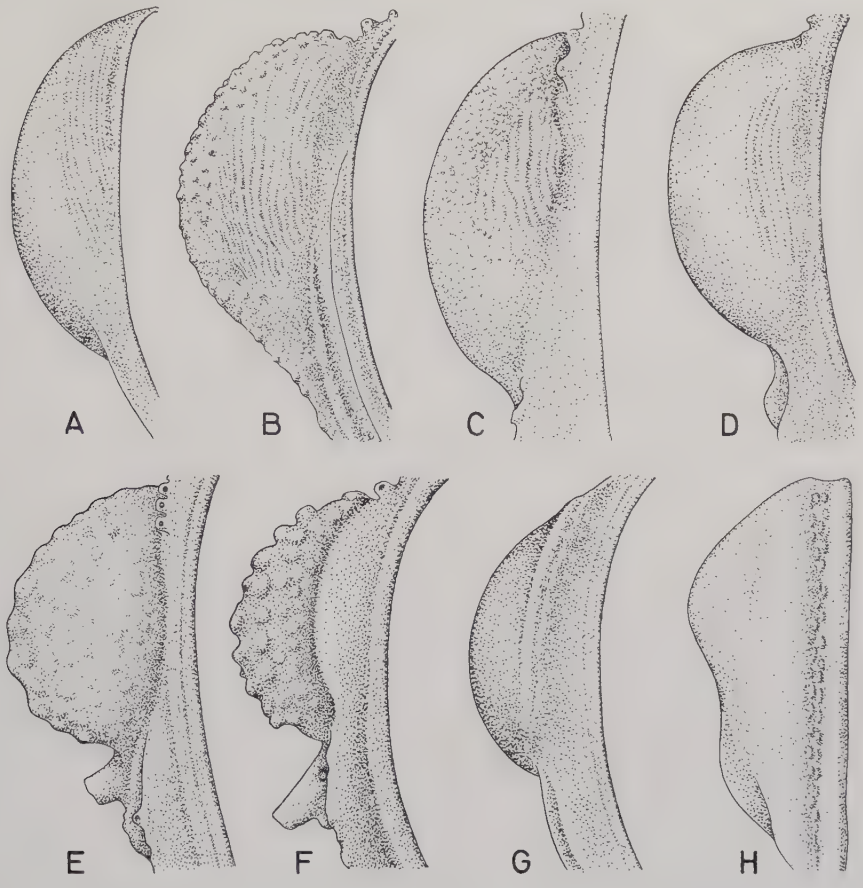


Fig. 140. Ventral morphology of the crumina in some representative *Beyrichiinae*. A. *Bingeria* n.g., drawing based on *B. zygophora* n.sp. B. *Beyrichia* (*Beyrichia*) (M'Coy 1846), based on *B. halliana* n.sp. C. *Beyrichia* (*Simplicibeyrichia*) n.subg., based on *B. globifera* n.sp. D. *Neobeyrichia* (*Nodibeyrichia*) (Henningsmoen 1954), based on *N. regnans* n.sp. E–F. *Calcaribeyrichia* n.g., based on *C. simplicior* n.sp. (E) and *C. bicalcarata* n.sp. (F). G. *Gannibeyrichia* n.g., based on *G. biplicata* n.sp. H. *Navibeyrichia* n.g., based on *N. balticivaga* n.sp. A ×30, B ×30, C ×45, D ×45, E ×35, F ×35, G ×40, H ×45.

paper) Matthew (1886) must be regarded as the author of the family-group names based on the genus *Beyrichia* (in forming the subfamily name *Beyrichinae* Matthew added a subfamily ending according to the rules of nomenclature but made the very common error of omitting the *i* which is the end of the stem; cf. *Kloedeninae* as introduced by Ulrich & Bassler 1923). Contemporaneously Sylvester-Bradley & Levinson (1960), without taking up Matthew's authorship for discussion (cf. Howe 1955, p. 18; Martinsson 1956, p. 18; Jaanusson 1957, p. 222; Kesling & Rogers 1957, p. 999), proposed the family name *Beyrichiidae* Ulrich 1894 to be added to the Official List of Family-Group Names in Zoology. However, the family-group name appeared even

as a quite correctly constructed family name before Ulrich 1894, viz. in Miller's (1889) handbook of North American geology and palaeontology (op. cit., p. 523).

Genus *Beyrichia* M'Coy 1846

Fig. 140B.

Type Species.—*Beyrichia Klödeni* M'Coy 1846
Subgenera.—*Beyrichia* (*Beyrichia*) M'Coy 1846
Beyrichia (*Altibeyrichia*) n.subg.
Beyrichia (*Scabribeyrichia*) n.subg.
Beyrichia (*Asperibeyrichia*) n.subg.
Beyrichia (*Simplicibeyrichia*) n.subg.
Beyrichia (*Lunulibeyrichia*) n.subg.

Diagnosis.—*Beyrichiinae* with an uninterrupted, more or less wide connection between the anterior lobe and the syllobium, without any lobular differentiation.

Remarks.—Other characters, with a few exceptions, keep this large group together. The syllobium is very broad and generally develops two cusps. There is generally a very well-developed striate field on the ventral side of the crumina. The anteroventral depression, if present at all, is never so large that it so much as tends to break the lobal connections below the preadductorial knob. The ornamentation is a granulation with tubercles and, mostly, relatively short spines. There is a shallow syllobial groove, and the calli, if present, are not very well developed.

The genus comprises one large subgenus with a very stable lobal pattern, *Beyrichia* (*Beyrichia*). Other associated species can be divided into small groups with only one or a few known representatives. They are generally very widely separated from each other, but their affinities to the subgenus *Beyrichia* (*Beyrichia*) are not characterized by considerable morphological discontinuities. They are regarded here as subgenera.

Subgenus *Beyrichia* (*Beyrichia*) M'Coy 1846

Fig. 140B.

Type Species.—*Beyrichia Klödeni* M'Coy 1846
Species.—*Beyrichia Klödeni* M'Coy 1846
Beyrichia (*Beyrichia*) *halliana* n.sp.
Beyrichia (*Beyrichia*) *eteliana* n.sp.
Beyrichia (*Beyrichia*) *ponderosa* n.sp.
Beyrichia bicuspis Kiesow 1888
Beyrichia (*Beyrichia*) *snoderiana* n.sp.
Beyrichia (*Beyrichia*) *hellviensis* n.sp.

Beyrichia (*Beyrichia*) *dactyloscopica* MARTINSSON 1956
Beyrichia verrucosa KOLMODIN 1869
Beyrichia (*Beyrichia*) *peponulifera* n.sp.
Beyrichia (*Beyrichia*) *morifera* n.sp.
Beyrichia (*Beyrichia*) *grogarniana* n.sp.
Beyrichia (*Beyrichia*) *arctigena* MARTINSSON 1960

DIAGNOSIS.—*Beyrichia* spp. with a well delimited crumina and a broad syllobium. Verrucose, tuberculate, or spinose, without other differentiations in the ornamentation of the lobes than the distinction of a supravelar field or row of tubercles, between a calcarine and an uncular tubercle or spine. Velum never higher than a ridge; syllobial groove not exceptionally high.

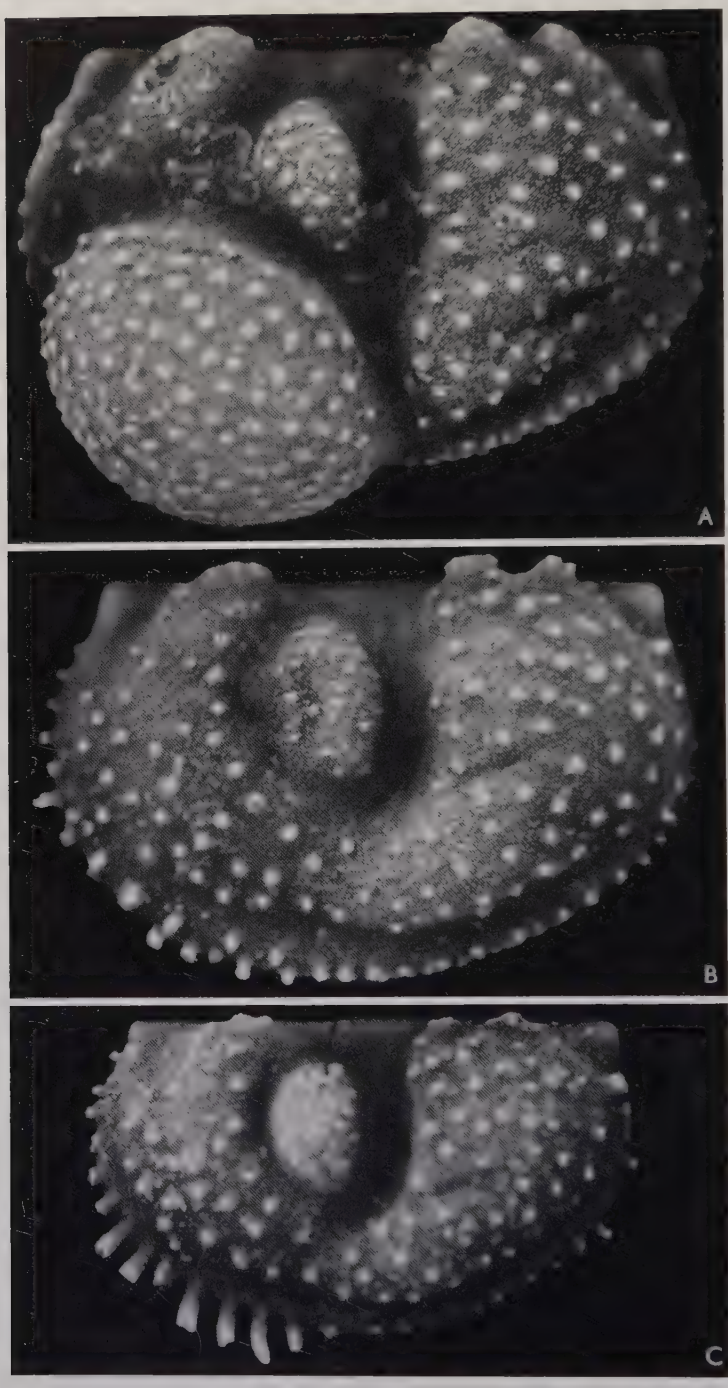
Beyrichia (*Beyrichia*) cf. *kloedeni* M'COY 1846

Fig. 1.

REMARKS.—*Beyrichia kloedeni* is the most important beyrichiid species from the point of view of nomenclature. Its taxionomic status is at present the following:

Since KESLING & WAGNER (1956) had presented their opinion that *B. kloedeni* is a junior and "stillborn" synonym of *Battus tuberculatus* KLÖDEN, which is not the case (MARTINSSON 1960c), lectotypes of these species were designated by SYLVESTER-BRADLEY & LEVINSON (1960). The lectotype of *B. kloedeni* is a right tecnomorphic valve, figured by STRAW 1928, Pl. I, fig. 1, from the same locality and collection as the material used by M'COY for his description.

This designation can only be firmly agreed with; the specimen in question is the only one known which could possibly even be identical with one of the tecnomorphic valves figured by M'COY (op. cit). However, it is an internal mould, and there is still room for suggestions that the outer surface of the valve might prove the synonymy of the species. In strong agreement with HENNINGSMOEN's (1954, p. 23) interpretation it should be stressed that the moulds in M'COY's material have filled valves of a species closely related to *Beyrichia* (*Beyrichia*) *halliana* n.sp., a Llandoverian—Wenlockian species. *B. tuberculata* as figured by KLÖDEN (1834, Pl. I, fig. 21) is conspecific with a very different beyrichiine excellently figured by KESLING & WAGNER 1956, occurring near the upper boundary of the Silurian of Europe. Corresponding complete valves of a Wenlockian species from the Welsh Borderland, which could possibly extend down into the Llandoverian and even be conspecific with *B. kloedeni* from Boocaun, are illustrated in Fig. 1 of this paper. With the existing material it is also impossible to distinguish the Llandoverian *Kloedenia obesa* HARPER 1940 from *B. kloedeni*; this species seems, however, to have had a relatively coarser reticulation than the specimens in Fig. 1 of this paper.



Female valve, No. G 531 (holotype).

Male valve, No. G 532.

Younger tecnomorph, No. G 533.

Fig. 141. *Beyrichia* (*Beyrichia*) *halliana* n.sp., Upper Visby Beds, Halls Huk. ×40.

Fig. 142. *Beyrichia* (*Beyrichia*) *halliana* n.sp., Upper Visby Beds, Irevik I, ventral view of right crumina; anterior end towards the upper right corner. No. G 534. × 60.

It is almost impossible to carry this identification further; the only attractive possibility is dependent on well preserved external moulds from the obviously non-calcareous type stratum in Galway.

Beyrichia (*Beyrichia*) *halliana* n.sp.

Figs. 141, 142, and 144.

Derivation of the Name.—Latin *Hallianus*, inhabitant of the parish of Hall, Gotland.

Holotype.—A left female valve, No. G 531 (Fig. 141 A).

Type Stratum and Type Locality.—Upper Visby Beds at Halls Huk, Gotland.

Diagnosis.—Large subamplete *Beyrichia* (*Beyrichia*) species with undifferentiated tuberculation on the lobes and on the crumina, large tubercles or spines anteroventrally on the tecnomorphic velar ridge, two subequal cusps on the syllobium, and a fine but distinct syllobial groove. No prominent uncular spine in adult specimens.

Description.—The general morphology of the lobes is best described by the figures. The cusps of the anterior lobe and the syllobium protrude over the hingeline, all to about equal height. There is a marked depression below the almost isolated preadductorial knob. The anteroventral depression is very inconsiderable.

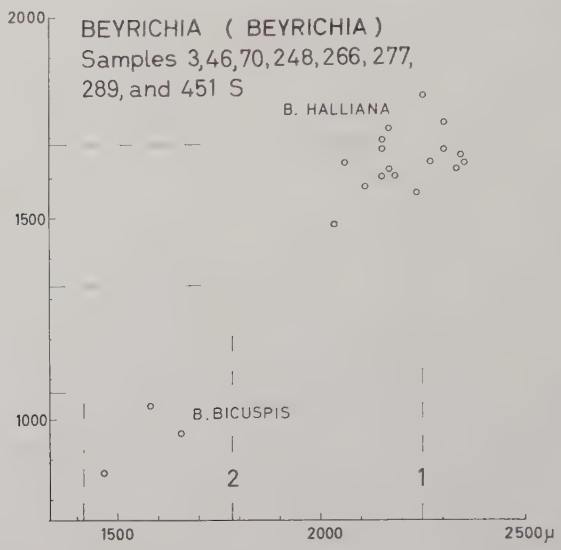


Fig. 143. Size dispersion of female specimens of two *Beyrichia* (*Beyrichia*) species living sympatrically in the Högklint Beds at Visby I. Hinge length plotted against sulcal height. Estimated average size of two earlier moult stages stated.

The ornamentation is an even granulosity with a superimposed tuberculation as described in the diagnosis. There is no marked obsoletion of the tuberculation even on the cuspidal part of the anterior lobe. If the syllobial tubercles below the groove are connected in rows—which is difficult owing to their random arrangement—they will form four or five such rows. Though all syllobial tubercles are of about the same size, it is rarely difficult to identify the uncular tubercle; seldom, and then only in younger tecnomorphs, does it become prominent (Fig. 141 C). Anteroventrally there is a velar row of higher tubercles and spines.

The striate field ventrally on the crumina is very well developed (Fig. 142). The ridge-like marginal structure is broken inside the crumina, and in this region the rounded fold between the margin and the crumina is very finely striate. The diffusely ridge-like torus disappears at this fold. The covering marginal frill is finely tubulous as in all other beyrichiines in which this structure has been exposed for investigation.

Dimensions.—The size variation at different localities is even greater than suggested by Fig. 144 which is composed of material from different strata. Unfortunately adult females are rare, and only sporadic figures can be given here (hinge length–sulcal height, in microns):

Lower Visby Beds, Nyhamn: 1975–1480. Upper Visby Beds, Halls Huk: 2215–1470, 2035–1500, 1875–1385; Irevik I: 2095–1430 1795–1320; Lickershamn I: 2045–1440; Snäckgärdsbaden: 2115–1675, 1910–1510. Högklint Beds, Visby I: 2395–1770. Tofta Beds, Annelund: 2415–1610. Slite Beds, Båta:

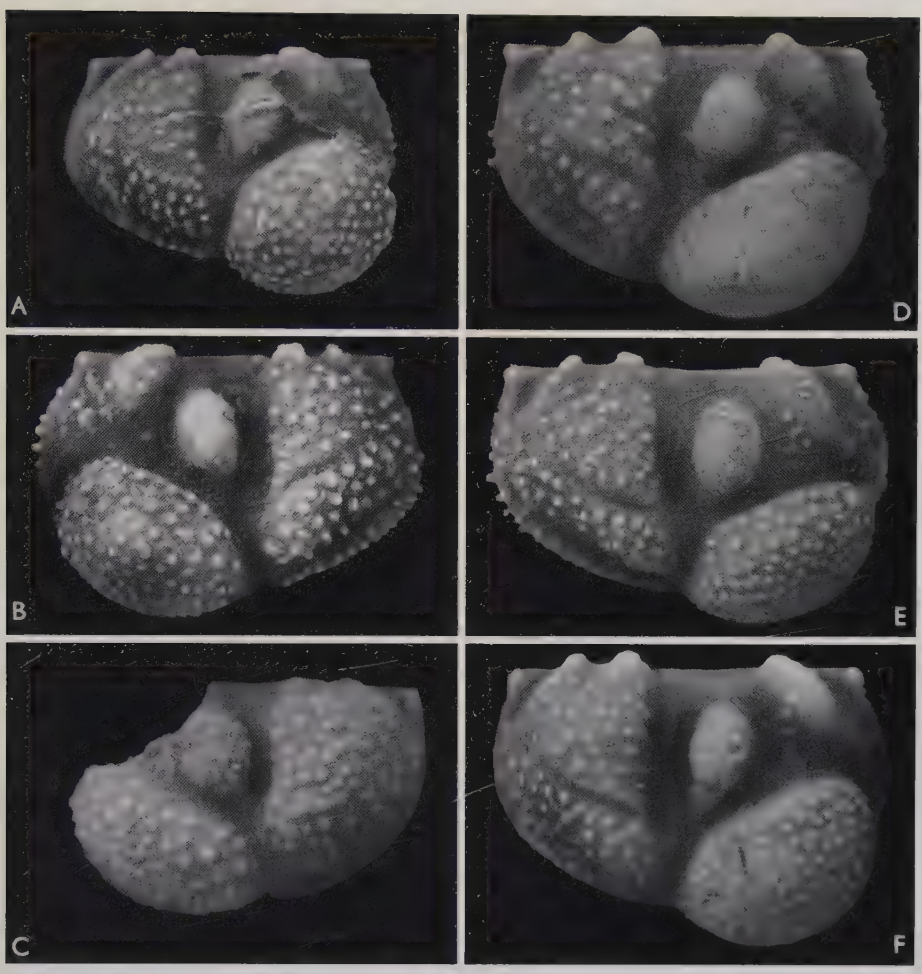


Fig. 144. *Beyrichia* (*Beyrichia*) *halliana* n.sp., female specimens from different stratigraphical levels. ×20. A. Lower Visby Beds, Nyhamn, No. G 535. B. Högklint Beds, Visby I, No. G 536. C. Tofta Beds, Galgberget, No. 537. D. Slite Beds, Båta, No. G 538. E. Slite Beds, Sinnarve, No. G 539. F. Slite Beds, Follingbo I, No. G 540.

2445–1400; Follingbo II: 2475–1745; Sinnarve: 1475–1710; Valbytte: 2750–1965. (Cf. also Figs. 143 and 163.)

Remarks.—The species is obviously very closely related to *B.* cf. *kloedeni* and *B. eteliana*; it does not have the uncular spines of these species or the very dense tuberculation of *B.* cf. *kloedeni*. It is morphologically very homogeneous all through its large stratigraphical range, except for the few adult specimens from the Tofta Beds which differ slightly in having a less well delimited crumina, less marked syllobial groove and cusps and in having a low callus along the groove. The size, however, steadily increases through the sequence. The

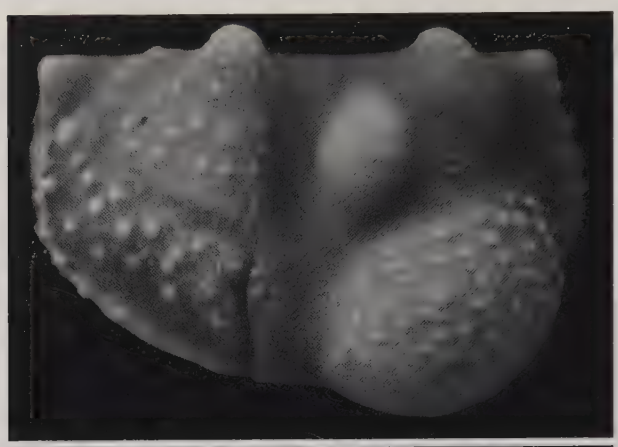


Fig. 145 A. *Beyrichia* (*Beyrichia*) *eteliana* n.sp., Hemse Beds, Tänglings. Female valve, No. G 541 (holotype). × 30.

Fig. 145 B. Same species and locality. Male valve, No. G 542. × 30.

species is stratigraphically well isolated from *B. eteliana* by the Halla, Mulde, Klinteberg and a large part of the Hemse Beds.

Occurrence.—Lower Visby Beds: Nyhamn, Nyhamn Well, Gustavsvik, Buske. Upper Visby Beds: Halls Huk, Irevik I, Lickershamn I, Snäckgärdsbaden, Ygne, Gnisvärd. Högklint Beds: Västös, Irevik II, Lickersham II, Visby I, Visby II. Tofta Beds: Annelund, Galgberget, Bingers. Slite Beds: Båta, Haganäs, Fårö Skola, Stuks, Stora Banne, Stora Myre, Yxne, Follingbo II, Oivide, Sinnarve, Valbytte.

Beyrichia (*Beyrichia*) *eteliana* n.sp.

Fig. 145.

Derivation of the Name.—Latin *Etelianus*, constructed from *Etel-* in the parish name of Etelhem.

Holotype.—A right female valve, No. G 541 (Fig. 145 A).

Type Stratum and Type Locality.—Hemse Beds at Tänglings, Gotland.

Diagnosis.—Large, not very conspicuously subamplete *Beyrichia* (*Beyrichia*)

species with almost undifferentiated tuberculation on the lobes and on the crumina, more finely tuberculate on the tecnomorphic velar ridge. The syllobium has two cusps, the anterior of them being considerably larger, and a fine syllobial groove. There is always a prominent uncular spine.

Description.—For the general morphology of the lobes and their ornamentation, see the Figures. The cusp of the anterior lobe and the anterior syllobial cusp are of about the same size and protrude considerably over the hingeline. The posterior syllobial cusp is very reduced, sometimes almost obsolete. The preadductorial knob is almost isolated; there is almost no depression at all in the region below it where the other lobal elements are united.

The granulose ornamentation with scattered tubercles is very similar to the conditions in the preceding species. There is a wide field of tubercles below the syllobial groove, without any differentiation of rows of larger tubercles. However, the preadductorial node has no coarser ornamentation than a low verrucosity, and the cuspidal part of the anterior lobe has very few tubercles.

Dimensions.—Hinge length of a female valve from Tänglings 2310 μ, sulcal height 1545 μ.

Remarks.—This species has the marked uncular spine in common with *B.* cf. *kloedeni* as described but differs from it by the much sparser tuberculation. It differs from *B. halliana* by the presence of the spine, by the less spinose velar ridge, and by lacking a depression below the preadductorial knob. It differs from both species in having relatively smaller crumina and preadductorial knob and by lacking coarse ornamentation on the preadductorial knob and also mainly on the cuspidal part of the anterior lobe.

Occurrence.—Hemse Beds: Tänglings. Though the species is not particularly rare and different moult stages are well represented, only one adult female specimen has been found.

Beyrichia (*Beyrichia*) *ponderosa* n.sp.

Fig. 146.

Derivation of the Name.—Latin *ponderosus*, weighty, referring to the voluminous size of the species.

Holotype.—A relatively small right female valve, No. G 543 (Fig. 146A).

Type Stratum and Type Locality.—Slite Beds at Vallstena, Gotland.

Diagnosis.—Very large subamplete *Beyrichia* (*Beyrichia*) species, granulose with a mostly inconsiderably marked verrucosity. Crumina longish; its base is concavely curved below the region of the preadductorial node and the prenodal sulcus. Two syllobial cusps of about the same size as the cusp of the anterior lobe.

Description.—The lobes fill out the lateral side of the valve, except for the sulci, almost completely, gently sloping down towards the velar bend; the cusps are rounded and not very prominent, though clearly protruding over the

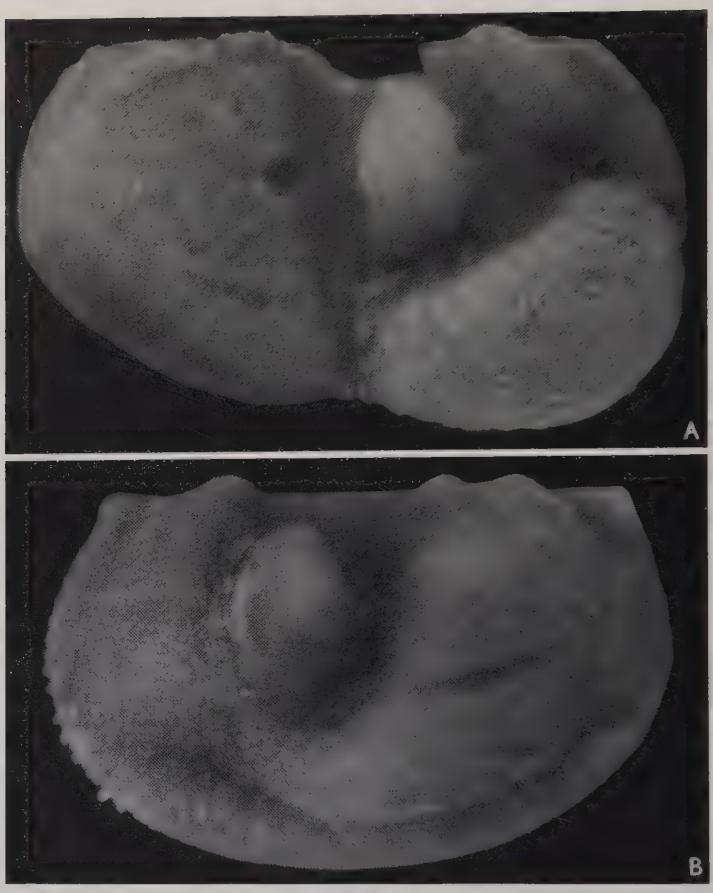


Fig. 146. *Beyrichia* (*Beyrichia*)*ponderosa* n.sp., Slite Beds. × 30. A. Female valve from Vallstena, No. G 543. B. Tecnomorphic valve from Gardrungs, No. G 544.

hingeline. There is a fine syllobial groove without or, less often, with a low callus. The preadductorial knob is almost isolated. Only the anteroventral part of the velar bend may be slightly tuberculate.

The species is subject to a considerable size variation; the verrucosity varies inconsiderably. The two specimens figured represent an average as to the verrucosity but belong in the lower part of the size range. It should be noted that the anteroventral depression in the tecnomorph figured is accidental; in no other tecnomorph is there any trace of a real anteroventral depression. Most specimens are distorted or incomplete in some way, probably partly due to the very large size in comparison with the thickness of the valve.

Dimensions.—Hinge length–sulcal height of female valves (measurements partly based on extrapolation of a missing cardinal corner):

Tofta Beds, Annelund: 2630 μ – 1685 μ. Slite Beds, Follingbo II: 2975 μ –

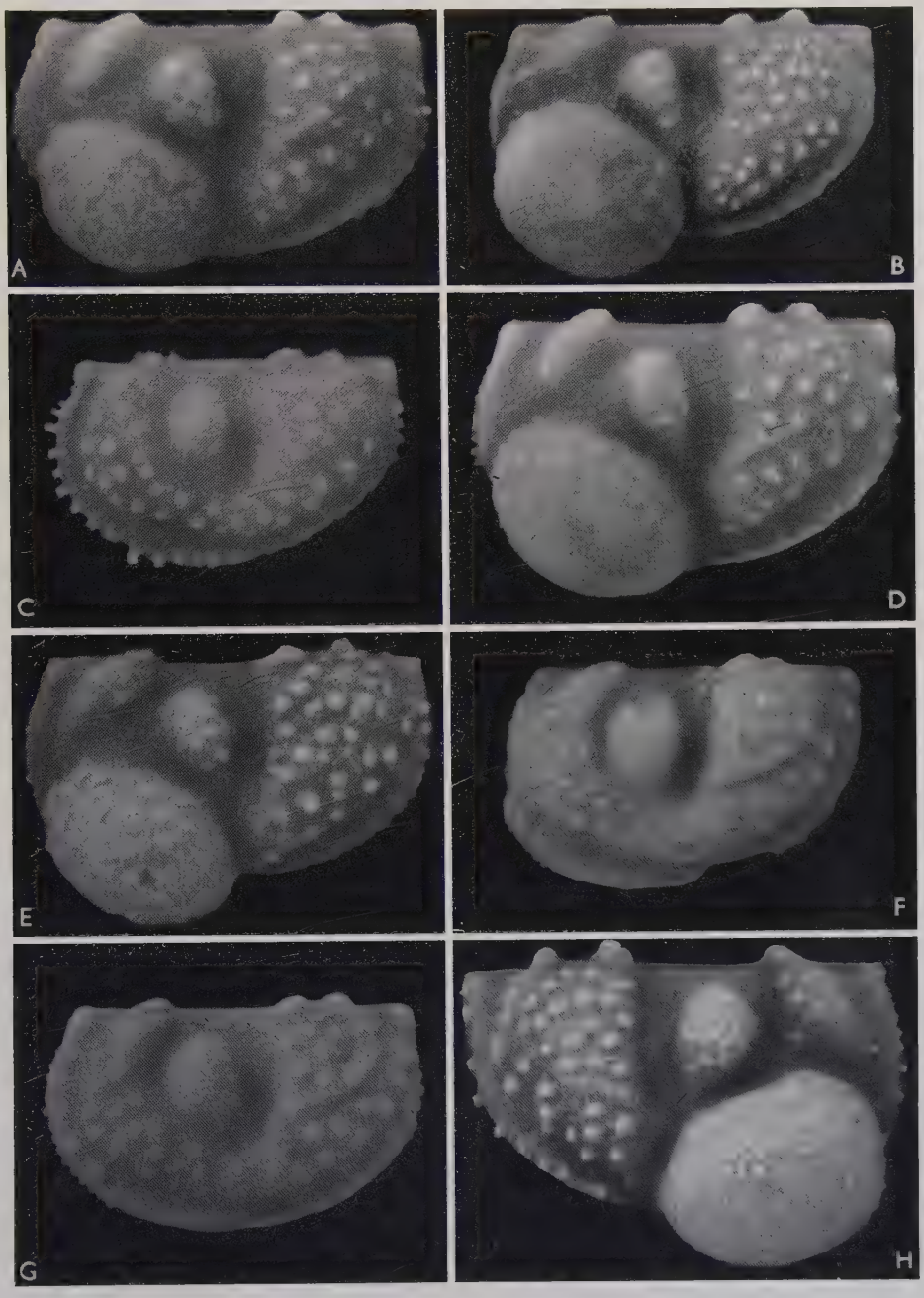


Fig. 147. *Beyrichia* (*Beyrichia*) *bicuspis* (Kiesow 1888). ×30. Females (A, B, D, E, and H), a possible case of incomplete cruminal metamorphosis, (F), and tecnomorphs (C and G) from different levels. A. Slite Beds, Stora Myre, No. G 545. B. Upper Visby Beds, Irevik I, No. G 546. C. Upper Visby Beds, Snäckgärdsbaden, No. G 547. D. Slite Beds, Båta, No. G 548. E. Högklint Beds, Visby I, No. G 549. F. Slite Beds, Follingbo I, No. G 261. G. Slite Beds, Stora Myre, No. G 551. H. Slite Beds, Follingbo I, No. G 552.

2030 μ; Vallstena: 2330 μ – 1630 μ; Slite (II ?, material, not exactly labelled, from the State Museum of Natural History): 2960 μ – 2230 μ.

Occurrence.—Tofta Beds: Annelund, Galgberget, Bingers. Slite Beds: Fårö skola, Oidehoburga, Broa, Alby, Längars, Hide, Slite II, Enholmen, Gane, Vallstena, Norrbys, Follingbo I, Follingbo II, Follingbo III, Nygårds, Gardrungs, Oivide.

Beyrichia (*Beyrichia*) *bicuspis* Kiesow 1888

Figs. 11 F and 147.

1888 *Beyrichia Klödeni* var. *bicuspis* mihi—Kiesow, p. 11; Pl. II, figs 6 and 7.
1954 *B. kloedeni* var. *bicuspis* Kiesow 1888—Henningsmoen, p. 24 (referred to the new subgenus *Beyrichia* (*Beyrichia*)).

Type Reference.—Lectotype designated herein, p. 29.

Diagnosis.—Medium-sized, subamplete or slighty preplete *Beyrichia* (*Beyrichia*) species with two subequal syllobial cusps; coarsely tuberculate without any differentiation of prominent rows of tubercles or spines. Shallow syllobial groove with no considerable callus.

Description.—All lobal cusps of about equal size, protruding over the hingeline. Preadductorial knob isolated; below it there is a depression in the connection between the anterior lobe and the syllobium; the shallow anteroventral depression slightly deflects the limit between the lobes and the velar ridge.

Tuberculation coarse, evenly distributed over all lobal parts of the carapace, except the cuspidal parts of the anterior lobe. In the field below the syllobial groove the tubercles can be connected by (2–)3–4 lines. The velum is set off from the lobal parts of the carapace as a distinct ridge, tuberculate or provided with short spines anteriorly, anteroventrally, and posteriorly. The crumina is mostly tuberculate or verrucose.

Dimensions.—Hinge length–sulcal height of female valves from the Slite Beds, in microns:

Follingbo I: 1950–1365, 1950–1310, 1930–1265, 1765–1205, 1745–1100. Stora Myre: 1675–1065, 1675–1130, 1650–1105, 1595–1045, 1500–1030. (See also Fig. 143).

Remarks.—The species has an unusually wide stratigraphical range and is subject to some variation at different localities; an extreme is shown in Fig. 147 H where the otherwise fairly stable subamplete outline has been abandoned for a more normally preplete outline in combination with an inconsiderably verrucose crumina. It has not been possible to establish any variational or qualitatively morphological limitation of these forms from the typical *B. bicuspis* as seen in the other figures.

This species is apparently closely related to the younger *B. snoderiana*, from which it differs mainly by the arrangement of the syllobial cusps, and with *B. hellviensis* which is a primitive representative of those *Beyrichia* (*Beyrichia*)

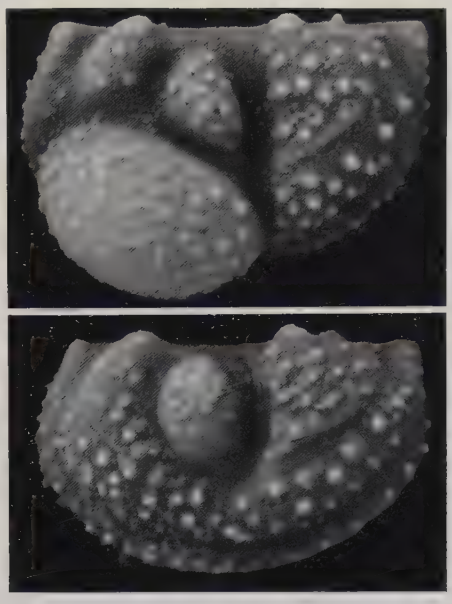


Fig. 148 A. *Beyrichia* (*Beyrichia*) *snoderiana* n.sp., Halla Beds, Möllbos. Female valve, No. G 553. × 30.

Fig. 148 B. Same species and locality. Male valve, No. G 554. × 30.

species which tend to reduce the posterior syllobial cusp and develop a differentiated field or row of tubercles below the syllobial groove. In *B. bicuspis* the relative density in the tuberculation or the verrucosity has decreased considerably as compared with the *Beyrichia* (*Beyrichia*) species described above, but there are no tendencies towards a differentiation of the kind mentioned.

Occurrence.—Upper Visby Beds: Irevik I, Lickershamn I, Snäckgärdsbaden, Ygne. Högklint Beds: Västös, Visby I, Ansarve. Tofta Beds: Annelund, Galgberget, Bingers. Slite Beds: Båta, Haganäs, Fårö skola, Oidehoburga, Stora Banne, Alby, Puttarsjaus, Längars, Hide, Slite I, Slite II, Enholmen, Gane, Vallstena, Stora Myre, Yxne, Käringen, Norrbys, Follingbo I, Follingbo II, Nygårds, Gardrungs, Oivide.

Beyrichia (*Beyrichia*) *snoderiana* n.sp.

Figs. 148–150.

Derivation of the Name.—Latin *Snoderianus*, inhabitant of Snoder, referring to the type locality.

Holotype.—A left female valve, No. G 558 (Fig. 150A).

Type Stratum and Type Locality.—Hemse Beds at Snoder, Gotland.

Diagnosis.—Medium-sized, preplete *Beyrichia* (*Beyrichia*) species in which the posterior syllobial cusp is entirely obsolete or not much larger than one of the lobal tubercles; coarsely tuberculate to verrucose without any differentiation of more prominent tubercles or spines. Syllobial groove generally well marked, mostly with a distinct callus along its upper margin.

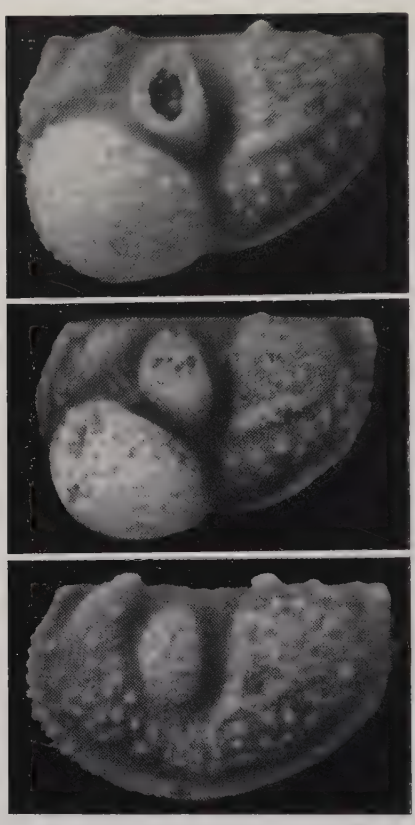


Fig. 149 A. *Beyrichia* (*Beyrichia*) *snoderiana* n.sp., Klinteberg Beds, Hunninge. Female valve, No. G 555. ×30.

Fig. 149 B. Same species, Mulde Beds, Däpps. Female valve, No. G 556. ×30.

Fig. 149 C. Same species and locality. Male valve, No. G 557. ×30.

Description.—The two well-developed lobal cusps protrude about equally over the hingeline. Preadductorial knob isolated; below it there is a depression in the connection between the anterior lobe and the syllobium; the shallow anteroventral depression often deflects the limit between the lobal part of the valve and the marked velar ridge.

Tuberculation coarse; sometimes, however, represented by only a sparse verrucosity; this ornamentation becomes sparser or obsolete on the cuspidal part of the anterior lobe. Three, or seldom four, connecting lines can be drawn between the tubercles in the supravelar field below the syllobial groove. The velum is tuberculate, or somewhat spinose, usually with exception of a portion ventrally and posteroventrally. The crumina is tuberculate or verrucose.

Dimensions.—Hinge length–sulcal height of female specimens, in microns: Halla Beds, Möllbos: 1810–1100, 1745–1180, 1730–1171, 1705–1120, 1705–1040. Hemse Beds, Snoder: 1835–1220, 1745–1150, 1685–1090, 1665–1100, 1635–1065.

Remarks.—As pointed out under the preceding species, with which it is closely related, this species mainly differs from it by the cuspidal part of the

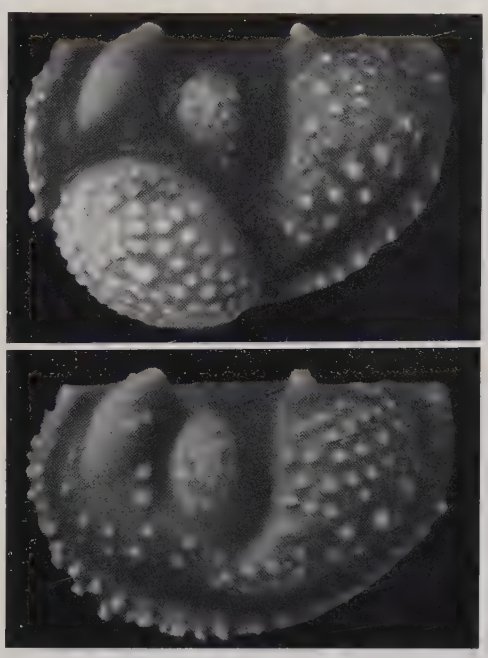


Fig. 150 A. *Beyrichia* (*Beyrichia*) *snoderiana* n.sp., Hemse Beds, Snoder. Female valve, No. G 558 (holotype). × 30.

Fig. 150 B. Same species and locality. Male valve, No. G 559. × 30.

syllobium. If forms like that in Fig. 147H are excluded, it is mostly readily distinguished from it in its general appearance by having a normal preplete outline with a gently curved posteroventral velar outline. Though the posterior syllobial cusp occasionally becomes more prominent, there are no transitional forms towards *B. bicuspis* as to this character.

As is often the case, certain features may make a part of this species characteristic to a minor stratigraphical unit and be traced horizontally within it for some distance. Thus material from the Halla Beds is characterized by its marked syllobial groove, material from the Mulde and Klinteberg Beds by its low tuberculosity or verrucosity and a low but marked callus, and from the Hemse Group by lacking these characteristics but having a more marked anteroventral depression than the others.

Occurrence.—Halla Beds: Hörsne, Gandarve, Möllbos. Mulde Beds: Däpps. Klinteberg Beds: Hunninge. Hemse Beds: Eske, Snoder, Hemmungs.

Beyrichia (*Beyrichia*) *hellviensis* n.sp.

Figs. 11E and 151.

Derivation of the Name.—Latin *Hellviensis*, inhabiting the parish of Hellvi, Gotland.

Holotype.—A left female valve, No. G 560 (Fig. 151A).

Type Stratum and Type Locality.—Slite Beds at Längars, Gotland.

Diagnosis.—Comparatively small *Beyrichia* (*Beyrichia*) species with one

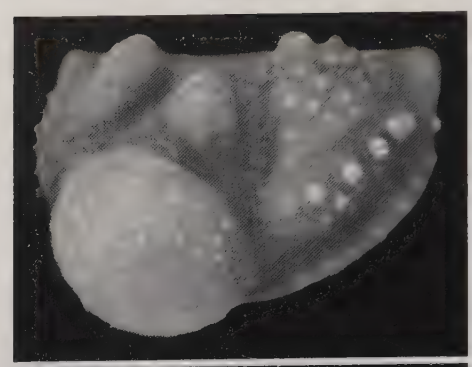


Fig. 151 A. *Beyrichia* (*Beyrichia*) *hellviensis* n.sp., Slite Beds, Hellvi. Female valve, No. G 560 (holotype). × 30.

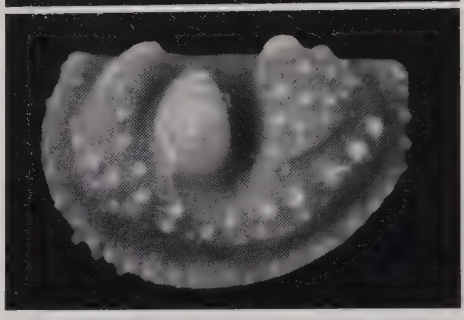


Fig. 151 B. Same species and locality. Tecnomorphic valve, No. G 561. × 30.

larger and one reduced syllobial cusp and a row of higher tubercles or small spines differentiated in the tuberculate field below the syllobial groove.

Description.—The cusp of the anterior lobe and the anterior syllobial cusp are about equal in size and protrude considerably over the hingeline. The large preadductorial knob is well isolated; there is a very shallow depression of the lobal connection below it. The velum is a well marked ridge, it is especially markedly set off from the lobal parts of the valve in the region of the anteroventral depression which is otherwise hardly discernible.

The ornamentation is a coarse tuberculation on the lobes, or rather a verrucosity on the preadductorial knob. The velar ridge is also tuberculate, verrucose, or even slightly spinose anteroventrally. The row of tubercles immediately below the syllobial groove is differentiated into higher units, often short spines, than other parts of the tuberculation of the lobes. This row ends with the calcarine and uncular tubercles, but these units are not more strongly developed than the three or four units between them. The crumina is finely and sparsely tuberculate.

Dimensions.—Hinge length–sulcal height of female specimens from Längars, in microns: 1625–1040, 1585–965, 1570–985, 1565–1000, 1555–1030.

Remarks.—This species shows clear relationships both to the preceding group of species and to the following but differs from all of them by the stage of differentiation to be found in the tubercular ornamentation of the supravelar syllobial field.

Occurrence.—Slite Beds: Alby, Längars, Hide, Slite II, Enholmen, Gane, Vallstena, Norrbys, Follingbo III. Possibly a small material, not further treated here, from Follingbo I, verrucose and with a much less developed syllobial cusp, belongs to this species.

Beyrichia (*Beyrichia*) *dactyloscopica* Martinsson 1956

Figs. 152 and 153.

1956 *Beyrichia* (*Beyrichia*) *dactyloscopica* n.sp.—Martinsson, p. 20; Pls. I–II, figs. 2–9.
1959 *Beyrichia dactyloscopica* Martinsson 1956—Pokorný, p. 327; Fig. 3; Pl. II.

Type Reference.—Cf. Martinsson 1956, p. 20.

Diagnosis.—Large, more or less spinose *Beyrichia* (*Beyrichia*) species with two syllobial cusps, the posterior one being considerably smaller. Syllobial groove under a very distinct callus; in the field below it the tubercles or spines from a fairly well-defined zone extending forwards onto the base of the anterior lobe; this zone tends to have more strongly developed ornamentation than other parts of the lobes. Preadductorial knob almost isolated; the depression in the lobal connection below it in the tecnomorphs is very shallow; the upper part of the base of the crumina is more or less concave.

Description.—As far as there is any low connection at all between the preadductorial knob and the syllobium, this is considerably narrower than the knob itself. The cusp of the anterior lobe and the anterior syllobial cusp are subequal in size and protrude over the hingeline.

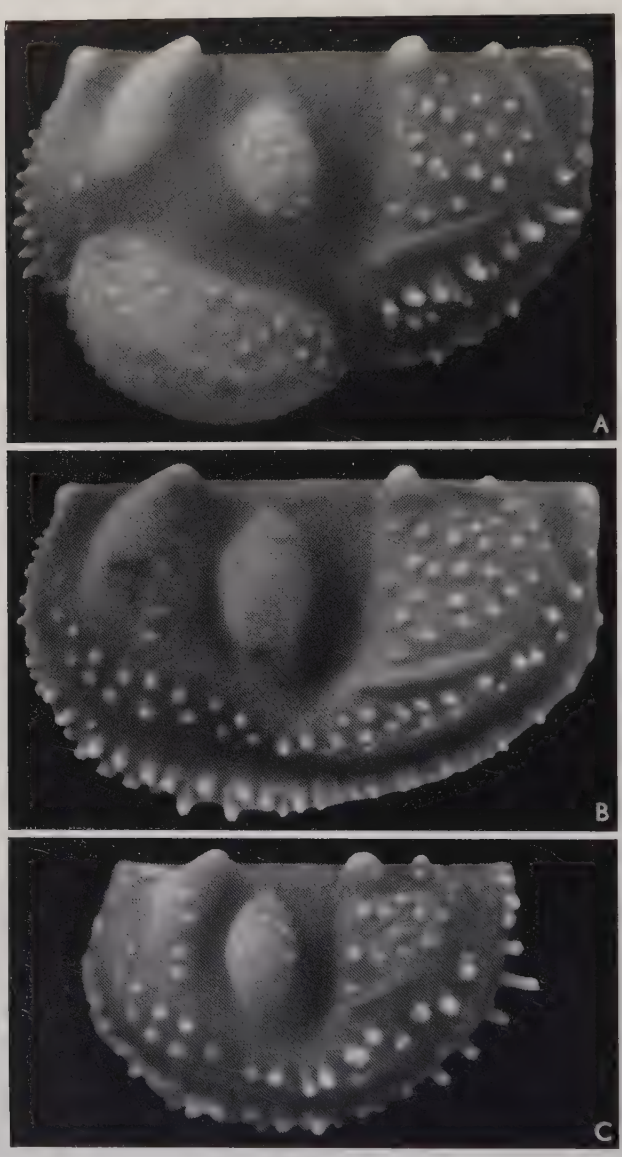
In addition to the supravelar zone mentioned in the diagnosis the upper parts of the syllobium are also tuberculate; the preadductorial knob is faintly tuberculate or distinctly verrucose, but the cuspidal part of the anterior lobe is entirely smooth or is provided with only a few tubercles. The crumina is sparsely tuberculate.

The anteroventral part of the well defined velar ridge is spinose; tubercles or spines, sometimes of considerable length, occur all along the velar edge.

Particularly interesting is the fact that the zone of tubercles below the syllobial groove tends to develop larger tubercles or long spines. The uncular spine—identified at the lower end of a very low ridge from the posterior syllobial cusp—is in these cases even smaller than the other spines, and the calcarine unit cannot be distinguished at all. This differentiation is very typical of the species as found in the Mulde Beds (Fig. 152), but in material from the Slite and Klinteberg Beds which must be regarded as conspecific, it is much less conspicuous if present at all.

Dimensions.—Hinge length–sulcal height of female valves from Mulde, in microns: 2510–1635, 2450–1585, 2445–1705, 2345–1485, 2250–1540.

Restriction of the Species.—Owing to the fact that the species is extremely rare at the type locality two other species. *B. peponulifera* and *B. morifera*, were included in *B. dactyloscopica*. If a preadult dimorphism existed in the



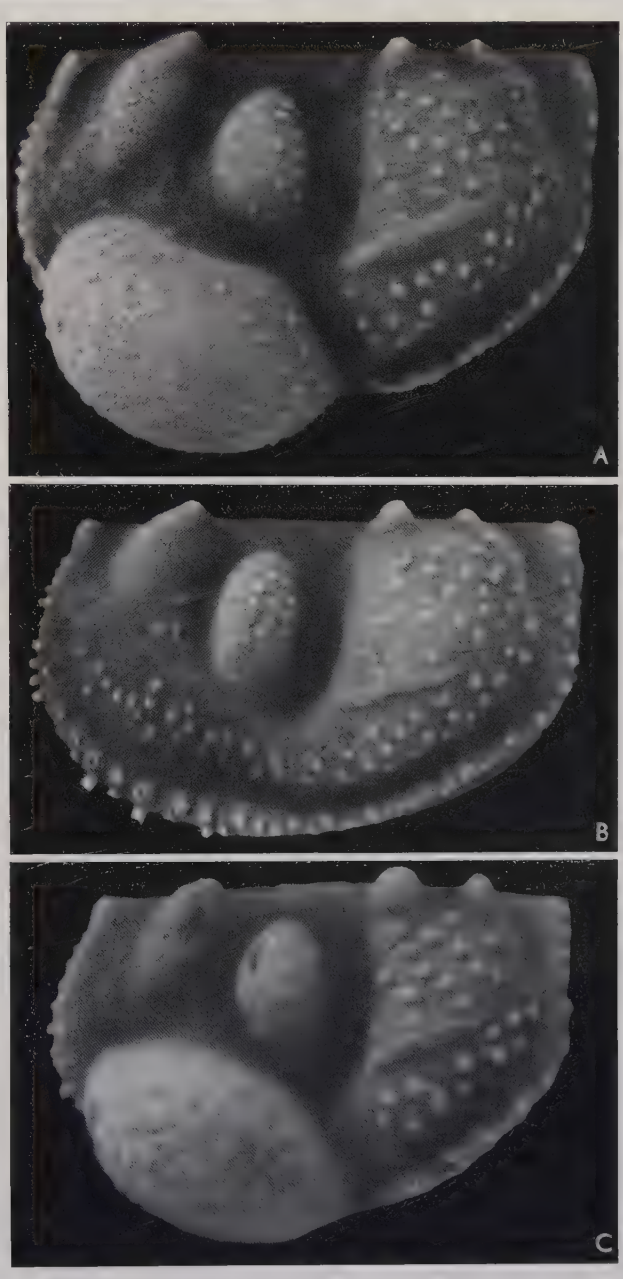
Female. Mulde Beds, Mulde, No. G 562. × 30.

Male. Mulde Beds, Mulde, No. G 563. × 30.

Tecnomorph. Mulde Beds, Mulde, No. G 564. × 30.

Fig. 152. *Beyrichia* (*Beyrichia*) *dactyloscopica* Martinsson 1956.

Beyrichiidae it cannot be excluded that the spinose zone in the normal female might be reduced to a simple row in cruminate specimens in younger moult stages. By now, however, it is established that there is a definite tendency to reduce the supravelar zone of spines into a single row, and it is now very questionable whether any cases of completed cruminal metamorphosis in preadult moult stages have been demonstrated at all.



Female. Slite Beds, Svarvare. No. G 565. × 30.

Male. Slite Beds, Svarvare. No. G 566. × 30.

Female. Klinteberg Beds, Hunninge. No. G 567. × 30.

Fig. 153. *Beyrichia* (*Beyrichia*) *dactyloscopica* MARTINSSON 1956.

By selective extraction of hundreds of kilograms of marl a material has been obtained which is sufficiently large to prove the smaller specimens to belong to two new species, *B. peponulifera* and *B. morifera*. This material now comprises 27 female specimens of *B. dactyloscopica*, 39 of *B. peponulifera*, and 11 of *B.*

morifera. These numbers also include numerous specimens obtained as contaminations in a material of adult *Craspedobolbina clavata* in the State Museum of Natural History, more or less selectively extracted during the last hundred years. The new species are described below.

Remarks.—Probably *B. dactyloscopica* is closely related to *B. verrucosa*. It differs from it by the morphology of the lobal cusps, the connection between the preadductorial knob and other lobal parts of valve, and, if the lectotype of *B. verrucosa* belongs to one of the later moult stages, by the general lateral outline of the valves. As proved by material from the Slite and Klinteberg Beds (Fig. 153) the ornamentation of the area below the syllobial groove in *B. dactyloscopica* is not more strongly developed than in *B. verrucosa*, but the tuberculation reaches so far onto the cuspidal part of the anterior lobe as in *B. verrucosa*.

Occurrence.—Slite Beds: Längars?, Puttarsjaus ?, Svarvare. Mulde Beds: Klintebys, Däpps, Mulde, Djupvik. Klinteberg Beds: Hunninge.

Beyrichia (*Beyrichia*) *verrucosa* (Kolmodin 1869)

Fig. 5C.

1869 *Beyrichia verrucosa* n.sp.—Kolmodin, p. 19; Fig. 12.

Type Reference.—Lectotype designated herein, p. 20.

Remarks.—Though much effort has been devoted to this problem, especially since *B. dactyloscopica* proved to occur without spinosity on the lobes, it has been impossible to establish the identity of this species and find adult females of it. There are three other fragmentary, smaller tecnomorphs in Kolmodin's original material besides the lectotype, but they only confirm the differences from *B. dactyloscopica* in the outline, syllobial cusps, and anterior tuberculation as stated under that species. None of the specimens has the callus typical of *B. dactyloscopica*. Probably the lectotype is an adult specimen. If the pieces of rock are not glacial erratics and come from existing expcsures in the neighbourhood of Gannarve, they are from the Slite or Mulde Beds.

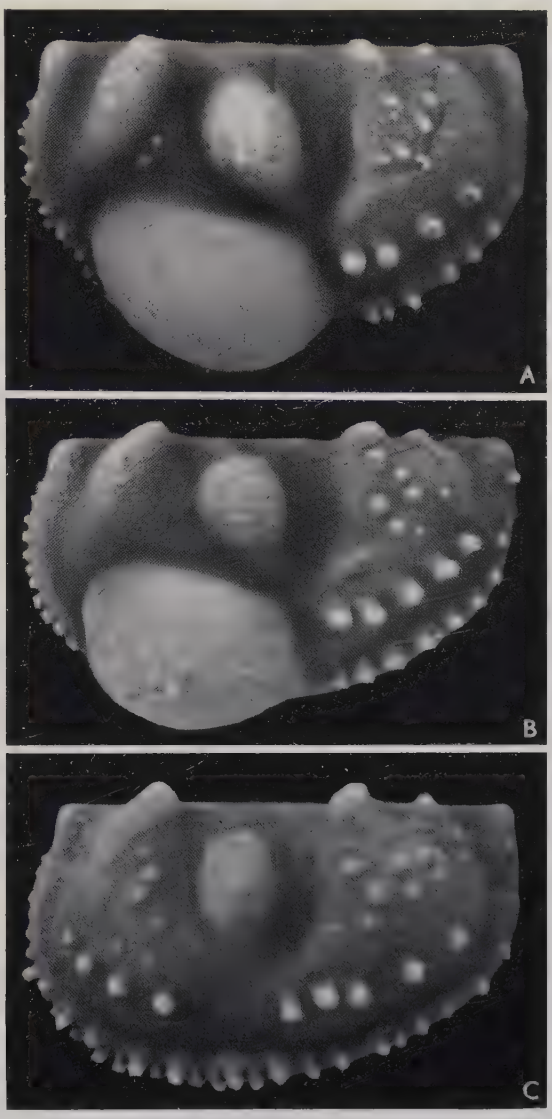
A species like the present can, even if the original has been identified, be saved as a serviceable taxionomic unit only provided the original material contains specimens enough to illustrate the morphology and variability of both dimorphs. *Beyrichia* (*Beyrichia*) *verrucosa* Kolmodin must still be treated as a *nomen dubium*.

Beyrichia (*Beyrichia*) *peponulifera* n.sp.

Fig. 154.

1956 *Beyrichia* (*Beyrichia*) *dactyloscopica* n.sp.—Martinsson, Pl. II, fig. 8.

Derivation of the Name.—Latin *peponulifer*, carrying a small pumpkin, referring to the crumina.



Female. Mulde Beds, Mulde. No. G 568. ×30.

Female. Mulde Beds, Mulde. No. G 569 (holotype). ×30.

Male. Mulde Beds, Mulde, No. G 570. ×30.

Fig. 154. *Beyrichia* (*Beyrichia*) *peponulifera* n.sp.

Holotype.—A left female valve, No. G 569 (Figs. 154B).

Type Stratum and Type Locality.—Mulde Beds at Mulde, Gotland.

Diagnosis.—Comparatively large *Beyrichia* (*Beyrichia*) species with two syllobial cusps, faintly marked syllobial groove and callus, one row of short spines below the groove, and a smooth or almost indiscernibly verrucose crumina.

Description.—The lobation is that typical of this group, with all lobal cusps well developed—the posterior syllobial cusp being smaller than the others—a

well isolated preadductorial knob, and a depression in the lobal connection below it. There is practically no anteroventral depression. In the female there is a low triangular elevation protruding from the lower part of the preadductorial node, but there is no real zygal connection with the syllobium.

Except for the supravelar row of spines, which is interrupted on the lobal connection below the preadductorial node, there is a low tuberculation or verrucosity on all other lobal parts; on the remaining cuspidal part of the female there are only a few tubercles or none at all. The velum has short spines or is tuberculate all around, more pronouncedly along the anteroventral and ventral parts.

The calcarine spine is somewhat higher situated than the other supravelar spine; probably the row does not include an uncular spine as it ends before reaching the very low uncular ridge.

Dimensions.—Hinge length–sulcal height of female specimens from Mulde, in microns: 2075–1205, 2075–1200, 2045–1210, 2045–1100, 2000–1185.

Remarks.—This species is closely related to *B. morifera* but differs from it by having a less preplete outline, shorter spinosity, lower and more rounded syllobial cusps, by its larger size, and by lacking tuberculation on the crumina.

Occurrence.—Slite Beds: Svarvare. Mulde Beds: Mulde.

Beyrichia (*Beyrichia*) *morifera* n.sp.

Figs. 155A–C.

1956 *Beyrichia* (*Beyrichia*) *dactyloscopica* n.sp.—Martinsson, Pl. I, fig. 4; Pl. II, fig. 9.

Derivation of the Name.—Latin *morifer*, carrying a mulberry, referring to the crumina.

Holotype.—A right female valve, No. G 572 (Fig. 155 B).

Type Stratum and Type Locality.—Mulde Beds at Mulde, Gotland.

Diagnosis.—Medium-sized *Beyrichia* (*Beyrichia*) species with two syllobial cusps, distinctly marked syllobial groove with a slightly bent callus, one supravelar row of long spines below the groove, and a coarsely tuberculate crumina.

Description.—The outline is strongly preplete. All lobal cusps protrude over the hingeline. The anterior syllobial cusp has conspicuously cylindrical sides and rounded top; the other two cusps are pointed. The anterior end of the callus is drawn down so that the structure becomes more or less sigmoid.

Except for the supravelar row of spines, which is not interrupted below the preadductorial node in the tecnomorphs, there are tubercles on the part of the syllobium above the groove, on the preadductorial node, on the cuspidal part of the anterior lobe (especially in the tecnomorph, more seldom in the female) and all over the crumina. The velar ridge is spinose along all its length. The calcarine spine is always distinguishable, the uncular never.

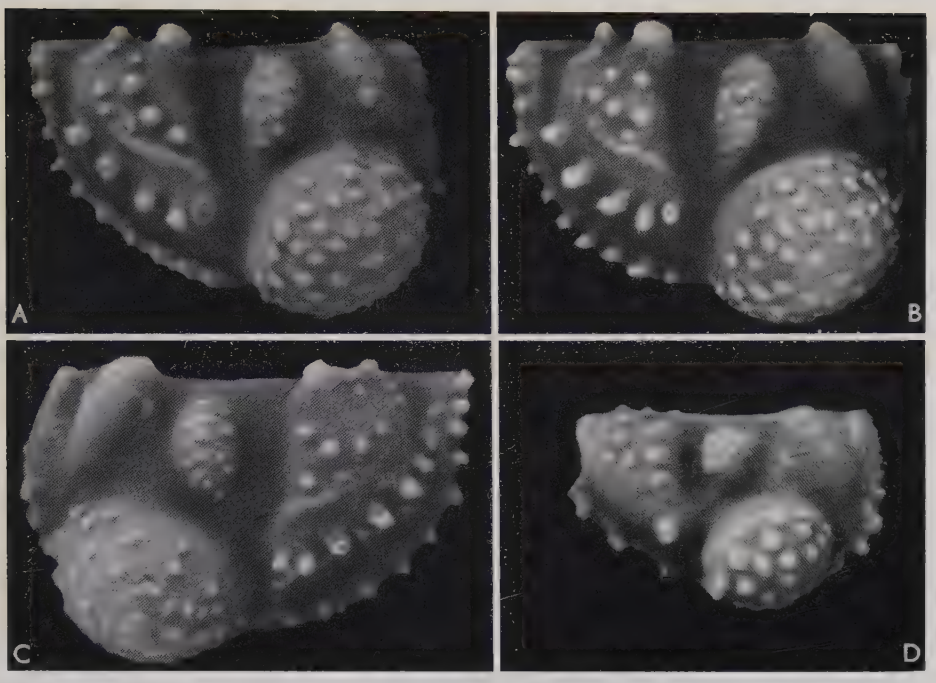


Fig. 155. A–C. *Beyrichia* (*Beyrichia*) *morifera* n.sp., Mulde Beds, Mulde. Female valves. ×30. A. No. G 571. B. No. G 572 (holotype). C. No. G 573. D. Problematic specimen (preadult dimorphism or new species) from the same locality. Female valve, No. G 574. ×30.

Dimensions.—Hinge length–sulcal height of female specimens from Mulde, in microns: 1830–1105, 1765–1145, 1755–1145, 1730–1130, 1625–1065.

Remarks.—This species is closely related to *B. peponulifera*; the main differences are stated under that species (p. 288).

The distinction of *B. peponulifera* and *B. morifera* from *B. dactyloscopica* implies that the last case of a possible preadult dimorphism in the *Beyrichiidae* suggested in previous literature has been eliminated. However, during the examination of the very extensive material from Mulde used for this study, one specimen appeared, looking as a preadult female of *B. morifera* could be expected to look. It is a perfectly developed female *Beyrichia* specimen (Fig. 155 D), with only a calcarine spine below the syllobial groove. It is remarkable that the high tubercles on the crumina do not point radially but more or less in lateral direction.

Occurrence.—Mulde Beds: Mulde (extremely rare, cf. p. 285), Blåhäll (common) Djupvik (common).

Beyrichia (*Beyrichia*) cf. s. aff. *morifera*

Fig. 156.

Remarks.—Three taxia which cannot be treated in detail owing to lack of material, have been found below and above the Mulde Beds. They have the

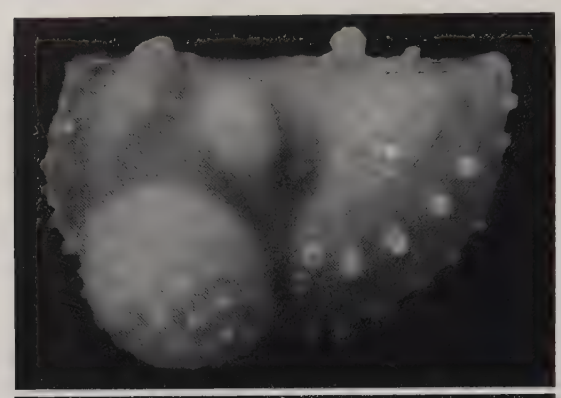


Fig. 156 A. *Beyrichia* (*Beyrichia*) cf. *morifera* n.sp., Klinteberg Beds, Hunninge. Female valve, No. G 575. × 40.

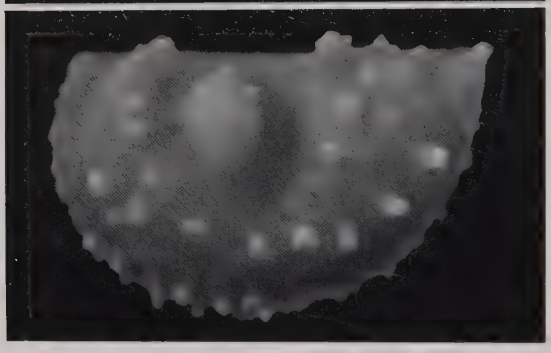


Fig. 156 B. Same species and locality. Tecnomorph, No. G 576. × 40.

same characteristics as *B. morifera* with respect to the supravelar row of spines and the ornamentation of the crumina but differ from it in other respects. They are briefly:

(A) *Beyrichia* (*Beyrichia*) aff. *morifera*. One, or possibly two, species from the Slite Beds: Längars (one tecnomorph), Hide (one tecnomorph), Gane (one female which cannot be proved to be conspecific with the others), Vallstena (one tecnomorph), Svarvare (one female and a few tecnomorphs). All are considerably larger than *B. morifera*, have a less preplete outline, pointed syllobial cusps and a very marked anteroventral depression; they lack the typical callus of *B. morifera*. The preadductorial knob is broadly connected with the lobes below it.

(B) *Beyrichia* (*Beyrichia*) cf. *morifera*. One fragmentary female valve with less pronounced syllobial groove, callus, and cruminal tuberculation than *B. morifera* but of the same size as the material from Mulde, from the Halla Beds at Hörsne.

(C) *Beyrichia* (*Beyrichia*) cf. *morifera*. A few small specimens of both sexes from the Klinteberg Beds at Hunninge (Fig. 156) agreeing completely with the diagnostic characters given for *B. morifera* except for the callus which is less well developed; the anterior syllobial cusp is yet more cylindrical than in the Mulde material; the cruminal tuberculation is somewhat less pronounced than in the Mulde material.

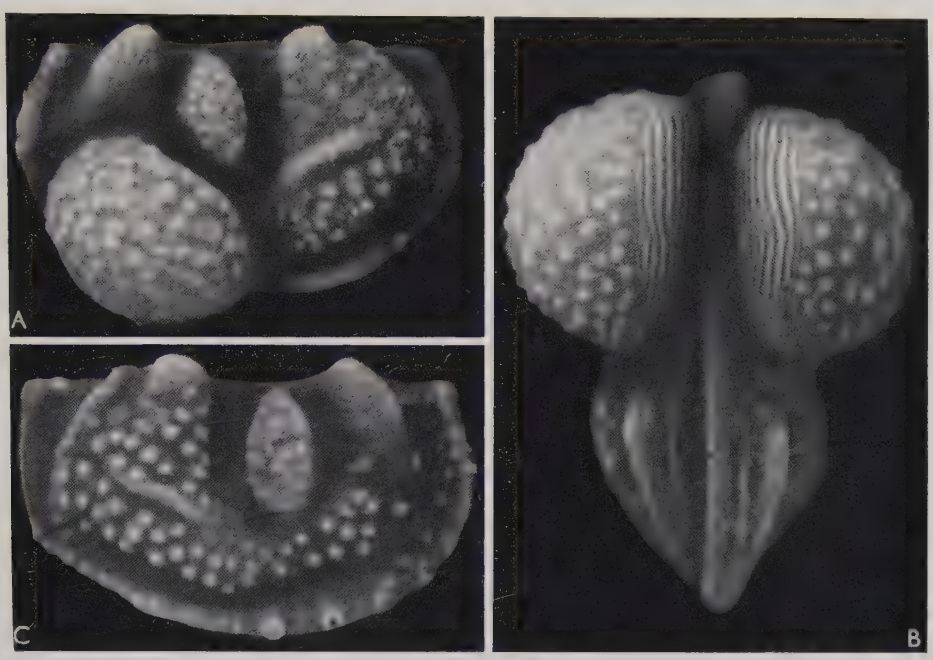


Fig. 157. *Beyrichia* (*Beyrichia*) *grogarniana* n.sp., Hemse Beds, Hammarudden. A. Female valve, No. G 577 (holotype) ×30. B. Female carapace, No. G 579. ×45. C. Male valve, No. G 578. ×30.

Beyrichia (*Beyrichia*) *grogarniana* n.sp.

Fig. 157.

Derivation of the Name.—Latin *Grogarnianus*, inhabiting the region of Grogarns and Grogarnsberget, Gotland.

Holotype.—A left female valve, No. G 577 (Fig. 157A).

Type Stratum and Type Locality.—Hemse Beds at Hammarudden, Gotland.

Diagnosis.—*Beyrichia* (*Beyrichia*) species with a high anterior syllobial cusp, equal in size to that of the anterior lobe. The posterior syllobial cusp is only the highest part of the uncular ridge which does not end in a spine or marked tubercle. Longish preadductorial knob. High callic ridge. No rows of larger tubercles or spines.

Description.—There is a shallow depression in the lobal connection below the isolated preadductorial knob. The outline of the velar ridge, which is well set off from the lobal parts of the valves and even somewhat constricted behind the crumina, is more or less sharply broken posteroventrally. There is no considerable anteroventral depression.

The velum has had a few longer, widely separated spines in a row anteroventrally. The broad syllobium and the preadductorial knob, as well as a supravelar

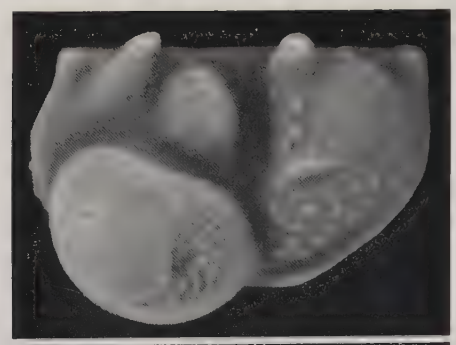


Fig. 158 A. *Beyrichia* (*Beyrichia*) *subornata* Martinsson 1956, Mulde Beds, Mulde. Female, No. G 580. ×30.

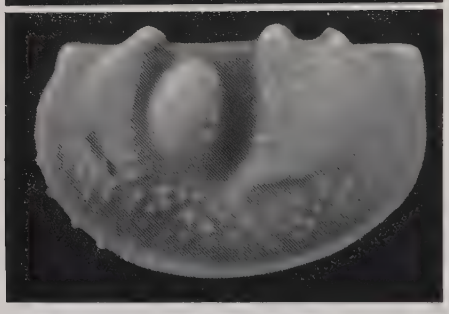


Fig. 158 B. Same species and locality. Male. No. G 581. ×30.

zone reaching onto the lower part of the anterior lobe are coarsely and densely tuberculate.

The crumina is densely tuberculate. The ventral morphology of the species is seen in Fig. 157 B. The granulosity and the superimposed tuberculation pass abruptly over into a coarse finger-print striation covering the inner ventral side of the crumina. As in most *Beyrichiinae* the torus is a simple low ridge near the margin.

Dimensions.—Hinge length–sulcal height of female specimens from Grogarns 2130 μ – 1245 μ, 1845 μ – 1200 μ; from Kaupungs 2090 μ – 1400 μ, 1945 μ – 1210 μ.

Remarks.—This, as well as the following species, represents a more independent development within the subgenus as compared with the two preceding groups with undifferentiated and differentiated tuberculation, respectively. The high callus in the dense syllobial tuberculation, the longish, isolated preadductorial knob, and the sparsely spinose velum are good differential characters in comparison with other *Beyrichia* (*Beyrichia*) species.

Occurrence.—Hemse Beds: Hammarudden, Grogarns, Kaupungs, Sigvalde.

Beyrichia (*Beyrichia*) *subornata* Martinsson 1956

Fig. 158.

1888 *Beyrichia Bolliana-umbonata* Reuter—Jones 1888a, p. 401; Pl. XXI, figs. 11 and 12.

1956 *Beyrichia* (*Beyrichia*) *subornata* n.sp.—Martinsson, p. 22; Pl. II, figs. 10–12.

TYPE REFERENCE.—Cf. MARTINSSON 1956, p. 22.

REMARKS.—The material of this very rare species from the Mulde Beds at Mulde has been considerably increased by the systematic selective extraction of larger specimens from this locality, so that 12 adult female specimens are known at present. New figures of the species are provided here (Fig. 158); as mentioned earlier (p. 27), two specimens of this species have been identified as originals used for illustrations by JONES (1888a).

Subgenus *Beyrichia* (*Altibeyrichia*) n. subg.

DERIVATION OF THE NAME.—Latin *altus*, high, and the generic name *Beyrichia*, referring to the shape of the carapace and the site of the syllobial groove.

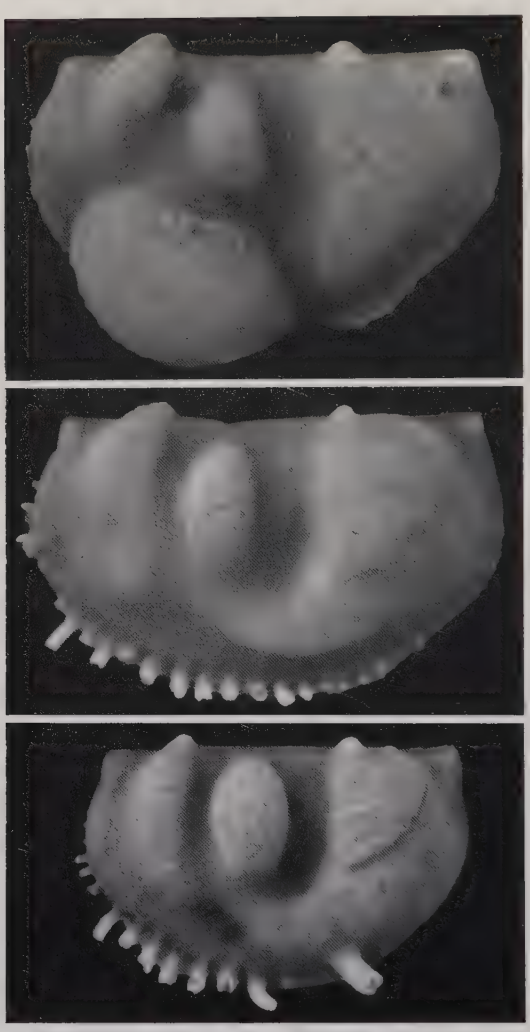
TYPE SPECIES.—*Beyrichia* (*Altibeyrichia*) *altiplancta* n.sp.

SPECIES.—*Beyrichia* (*Altibeyrichia*) *contracta* n.sp.
Beyrichia (*Altibeyrichia*) *altiplancta* n.sp.
Beyrichia (*Beyrichia*) *kiaeri* HENNINGSMOEN 1954.

DIAGNOSIS.—Subamplete, medium-sized *Beyrichia* species with a proportionally high carapace. The granulation of the lobes is broken only by a slight verrucosity, but a long calcarine spine occurs, especially in younger tecnomorphs; velar edge with a row of long spines. The anterior lobe tends to become isolated; the preadductorial knob is isolated or connected by a much lower lobal ridge with the supravelar portion of the syllobium. The anterior end of the syllobial groove is at or, mostly, much higher than the lower end of the sulcus.

REMARKS.—These species represent a line of lobal development which has many features of that in *Neobeyrichia* and which possibly leads to forms such as *Beyrichia* (*Neobeyrichia*) *ringerikensis* HENNINGSMOEN 1954. There is a strong reduction or, more frequently, an obsoletion of the posterior syllobial cusp. The anteroventral depression is considerable and almost connected with the prenodal sulcus, or else this part of the valve is flattened so that the cuspidal part of the anterior lobe becomes obsolete.

The consequence of the high position of the syllobial groove is in some species that the low lobal connection between the well marked preadductorial knob and the syllobium, which is superficially similar to a very wide zygal ridge, passes into the supravelar part of the syllobium, below the groove. This development, too, reaches an extreme in *B. ringerikensis*. As the morphology of the female of *B. ringerikensis* is not fully illustrated by the existing material, its subgeneric position is not further treated here. Attention should, however, be drawn to the fact that pronounced trends towards a lobation of *Neobeyrichia* type are found in three different lines within *Beyrichia*, distinguished here as the subgenera *Beyrichia* (*Altibeyrichia*), *Beyrichia* (*Simplicibeyrichia*), and



A. Female. Slite Beds, Follingbo I. No. G 582 (holotype). × 30.

B. Male. Slite Beds, Follingbo I. No. G 583. × 30.

C. Tecnomorph. Slite Beds, Follingbo I. No. G 584. × 30.

Fig. 159. *Beyrichia* (*Altibeyrichia*) *contracta* n.sp.

Beyrichia (*Lunulibeyrichia*). In the first of these subgenera the subamplete outline and the broad, sometimes bicuspidate syllobium indicate closer relationships to *Beyrichia* (*Beyrichia*) than to *Neobeyrichia*.

Beyrichia (*Altibeyrichia*) *contracta* n.sp.

Figs 159 and 160.

Derivation of the Name.—Latin *contractus*, contracted, referring to the short and high carapace.

Holotype.—A left female valve, No. G 582 (Fig. 159A).

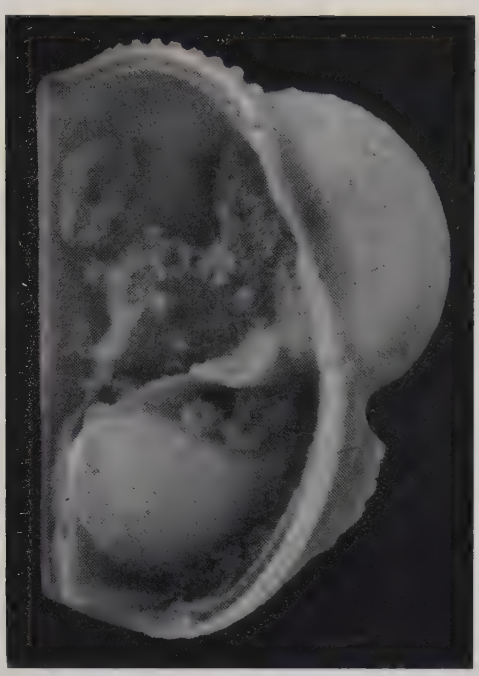


Fig. 160. *Beyrichia* (*Altibeyrichia*) *contracta* n.sp., Slite Beds, Follingbo I. Female valve in oblique ventral view, showing the ventral morphology of the velum and the crumina. No. G 585. ×40.

Type Stratum and Type Locality.—Slite Beds at Follingbo I, Gotland.

Diagnosis.—Very indistinctly verrucose *Beyrichia* (*Altibeyrichia*) species with a distinct anteroventral depression, long spines along the anteroventral and ventral parts of the velum in the tecnomorphs, and a short, wing-like postcruminal velar portion in the female. The syllobium is as a rule unicuspidate, though a rudimentary posterior syllobial cusp may appear even in adult specimens of both sexes.

Description.—The anterior lobe is connected with the other lobal elements by a low but broad elevation in the lower part of the prenodal sulcus; the anteroventral depression is deeper than in any other *Beyrichia* species. The lobal cusps protrude over the hingeline; especially in small moult stages there is often a small but distinct posterior syllobial cusp. The syllobial groove usually ends at some distance above the lower end of the adductorial sulcus or even at the same level as this end as in Fig. 159B.

The distinctly ridge-like and comparatively high velum has one row of spines which are very well-developed anteroventrally and ventrally in the tecnomorphs; the constriction of the velum leading to the formation of a wing-like postcruminal velar portion is seen in Fig. 160. The finger-print pattern of the crumina and the finely ridge-like torus are seen in the same figure.

The lobal ornamentation consists of a very low verrucosity; in the material from Follingbo figured here the granulation characteristic of all *Beyrichia* species is not seen. Often there is a long calcarine spine in the tecnomorphs,

Female. Mulde Beds, Däpps. No. G 586 (holotype). × 30.

Male. Mulde Beds, Däpps. No. G 587. × 30.

Fig. 161. *Beyrichia* (*Altibeyrichia*) *altiplancta* n.sp.

but there are never any additional higher tubercles or spines on the lobes (cf. Fig. 159C).

Dimensions.—Hinge length–sulcal height of female valves from Follingbo I, in microns: 1965–1160, 1850–1265, 1750–1220, 1705–1185, 1675–1165.

Remarks.—This species differs from *B. altiplancta* especially by the antero-ventral lobal morphology and by the spinosity of the velum. It has these features in common with *B. kiaeri* but differs from it by the stronger reduction of the syllobial cusps, the absence of larger tubercles, and, probably, by the wing-shaped female velar ridge.

Occurrence.—Slite Beds: Fårö Skola (?, more strongly verrucose than stated in the description), Alby, Slite I, Gane, Norrbys, Follingbo I, Follingbo II, Follingbo III, Stave, Gardrungs.

Beyrichia (*Altibeyrichia*) *altiplancta* n.sp.

Fig. 161.

Derivation of the Name.—Latin *altus*, high, and *plangere*, strike, hit, referring to the position of the syllobial groove.

HOLOTYPE.—A left female valve, No. G 586 (Fig. 161 A).

TYPE STRATUM AND TYPE LOCALITY.—Mulde Beds at Däpps, Gotland.

DIAGNOSIS.—*Beyrichia* (*Altibeyrichia*) species with a flattened area anteroventrally, comprising the lower part of the anterior lobe and the region of the anteroventral depression.

DESCRIPTION.—In the tecnomorphic anterior lobe only the cuspidal part is set off as a distinct lobal feature. The preadductorial node is almost completely isolated. The syllobium is broadly triangular with one stout cusp; there are almost no traces of its posterior cusp. The velum is not well set off from the lobal part of the valve; it has a row of spines anteroventrally and few spines or tubercles posteroventrally. There is a slight constriction of the velar ridge behind the crumina. The anterior end of the syllobial groove is situated considerably higher up than the lower end of the adductorial sulcus.

Except for the usual granulation, the ornamentation consists of a verrucosity, best seen on the syllobium and on the flattened anteroventral lobal area.

DIMENSIONS.—Hinge length–sulcal height of female specimens from Däpps: 2435 μ – 1795 μ, 2295 μ – 1670 μ, 2130 μ – 1635 μ.

REMARKS.—This species differs from the other species of the subgenus mainly by the flattened lobal area anteroventrally, implying the isolation of the cuspidal part of the anterior lobe and the lack of any kind of a lobal connection between the lower part of the syllobium and the preadductorial knob.

OCCURRENCE.—Mulde Beds: Däpps.

Subgenus *Beyrichia* (*Scabribeyrichia*) n. subg.

DERIVATION OF THE NAME.—Latin *scaber*, rough —referring to the ornamentation of the carapace—and the generic name *Beyrichia*.

TYPE SPECIES.—*Beyrichia tuberculata* var. *foliosa* JONES 1888.

SPECIES.—*Beyrichia* (*Scabribeyrichia*) *hirsuta* n.sp.

Beyrichia tuberculata var. *foliosa* JONES 1888.

DIAGNOSIS.—*Beyrichia* species with a distinct zygal arch in the tecnomorphs, not considerably affected by the inflation of the crumina in the female, and with advanced differentiation of the supravelar syllobial tuberculation into a field or row of tubercles or spines below the syllobial groove.

REMARKS.—The recognition of the zygal ridge as a primitive feature in the beyrichiid morphology has put its stamp on large parts of HENNINGSMOEN's (1954, 1955) treatment of the beyrichiid system. As far as the *Beyrichiinae* are concerned, this is especially obvious in *Eobeyrichia* (introduced as a subgenus by HENNINGSMOEN 1954) in which a zygal arch exists even in the adult female. In other words this also means that the incorporation with the crumina of parts of the valve wall had not proceeded so far that the zygal ridge was affected by the inflation of the crumina.

The present subgenus takes us back to a stage in the development of *Beyrichia* in which the zygal arch had not yet become obsolete in the tecnomorphs

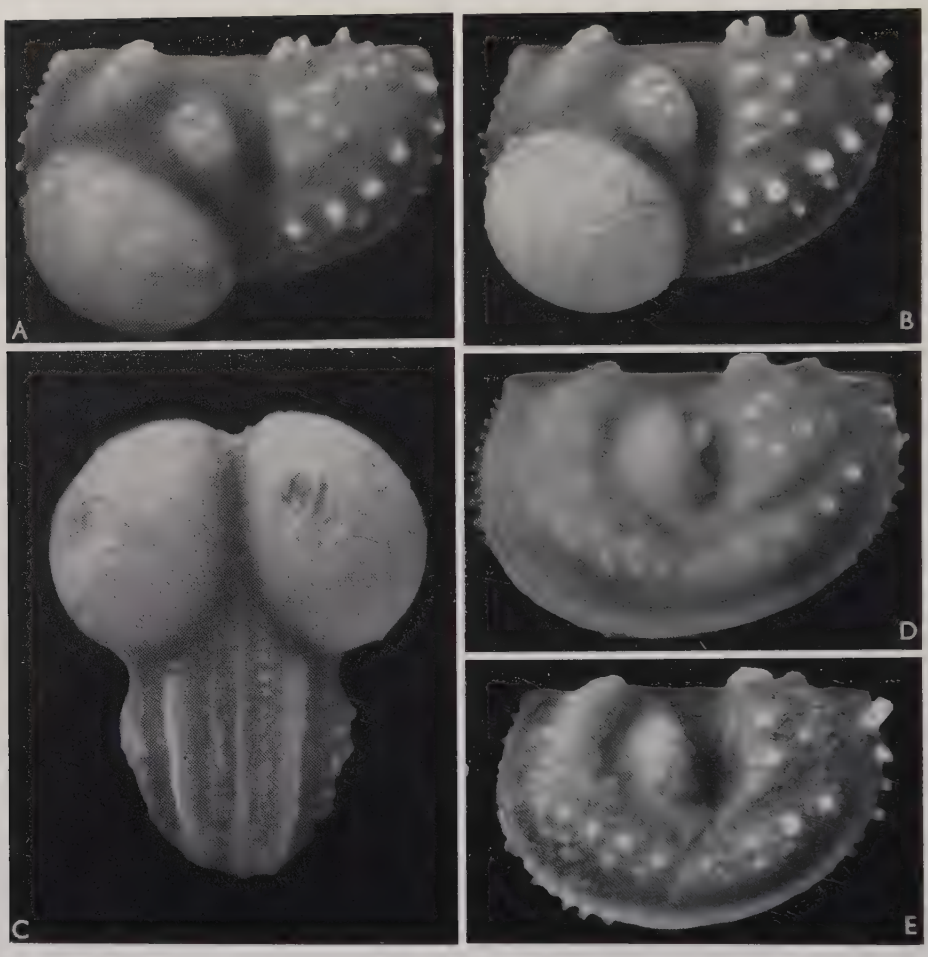


Fig. 162. *Beyrichia* (*Scabribeyrichia*) *hirsuta* n.sp., Lower Visby Beds, Nyhamn. × 40. A. Female, No. G 588. B. Female, No. G 589 (holotype). C. Female carapace in ventral view (anterior end up), No. G 590. D. Tecnomorph, No. G 591. E. Tecnomorph, No. G 592.

but where the trends towards a simplification or specialization of the supravelar tuberculation, as also known from *Beyrichia* (*Beyrichia*), had already appeared. Even in the cruminate carapace the zygal arch can be more or less well traced, primarily owing to the very markedly anterior position of the crumina.

The rareness of the *Beyrichia* (*Scabribeyrichia*) species has led to some caution as to the taxionomic treatment of the species; it is not known what importance the varying degree of specialization in the supravelar ornamentation might have in providing specific characters.

Beyrichia (*Scabribeyrichia*) *hirsuta* n.sp.

Figs. 162 and 163.

Derivation of the Name.—Latin *hirsutus* rough, spinose.

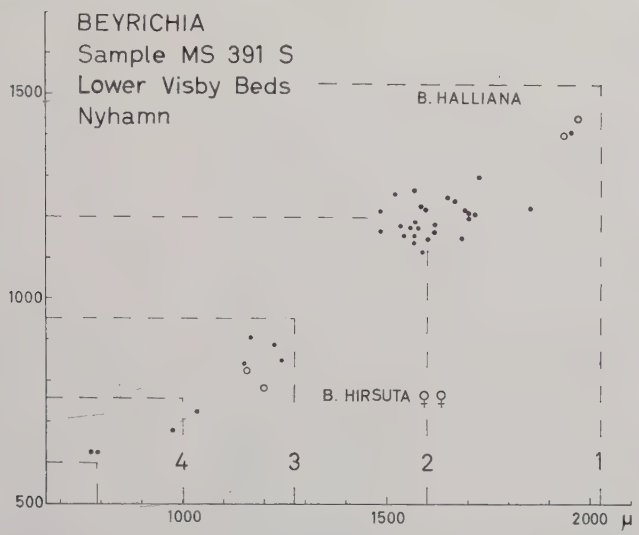


Fig. 163. Size dispersion (hinge length plotted against sulcal height) of *Beyrichia* specimens in a sample containing *Beyrichia* (*Beyrichia*) *halliana* n.sp. and *Beyrichia* (*Scabribeyrichia*) *hirsuta* n.sp. Estimated average growth rates for *Beyrichia halliana*, based on the penultimate moult stage, drawn as dashed lines.

Holotype.—A left female valve, No. G 589 (Fig. 162B).

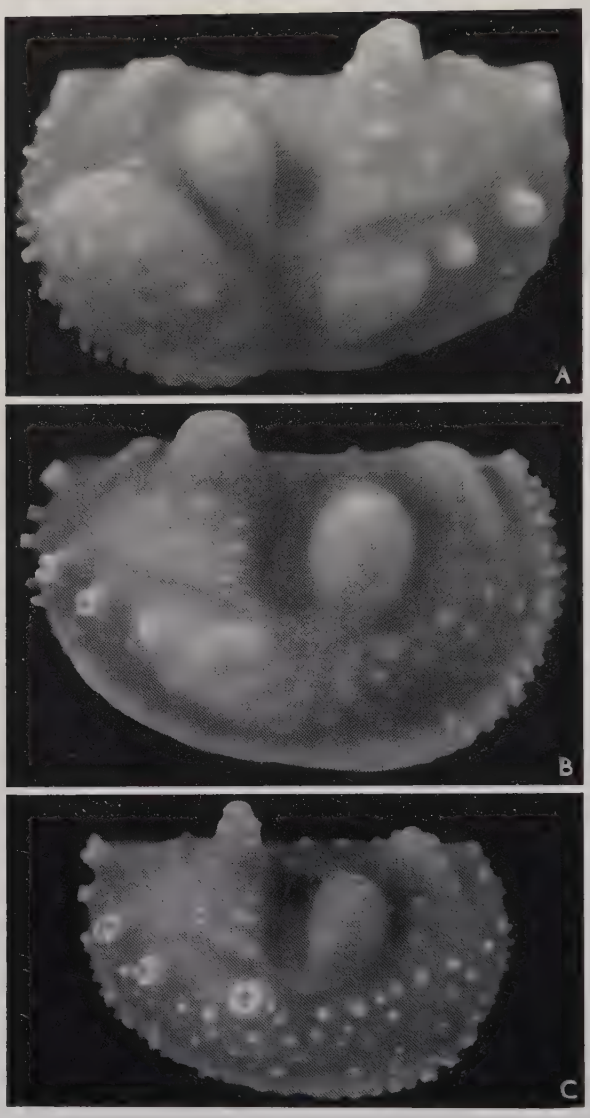
Type Stratum and Type Locality.—Lower Visby Beds at Nyhamn, Gotland.

Diagnosis.—Small *Beyrichia* (*Scabribeyrichia*) species with a row of longer spines in the supravelar field of the syllobium but without a thickening caused by fusion of tubercles in the region of the calcarine tubercle or tubercles.

Description.—The dimorphism does not only influence the cruminal part of the valve but also considerable parts of the lobal ornamentation.

In the tecnomorphs there is a clearly discernible zygal arch (Fig. 162D). The anterior lobe and the lower part of the syllobium are connected below the zygal arch, and there is no anteroventral depression. The lobal cusps protrude over the hingeline; the anterior of the syllobial cusp is stout and truncate, the posterior is smaller and more pointed. The velum is a well marked ridge. The lobal surfaces are sparsely tuberculate; there is a tendency in the row of tubercles below the syllobial groove to become larger, but there is no unit in this row which really attains the length of a spine, except the uncular spine. The velum is tuberculate or has short spines.

The adult female has a markedly anterior crumina which slightly displaces the zygal arch; this structure is traceable but not very distinct. The cuspidal part of the anterior lobe is similar to that in the tecnomorphs, but the syllobial cusps are covered or crowned by spines or high tubercles. All syllobial tubercles are very high, often prolonged as spines, and the supravelar row of spines is very well developed; an uncular and sometimes a calcarine spine are conspicuous. There are also a few spines in the area below this row.



Female. Slite Beds, Enholmen. RM No. Ar 25888:3. ×30.

Tecnomorph. Slite Beds, Follingbo III. No. G 593. ×30.

Younger tecnomorph. Slite Beds. Follingbo III. No. G 594. ×30.

Fig. 164. *Beyrichia* (*Scabribeyrichia*) *foliosa* (Jones 1888).

The ventral morphology of the crumina, as far as it has been made accessible (Fig. 162C) is very similar to that in other subgenera of *Beyrichia*, but it is noteworthy that the torus behind the crumina is dissolved into a row of tubercular units.

Dimensions.—Hinge length–sulcal height of female valves from Nyhamn: 1280 μ – 850 μ, 1220 μ – 865 μ. Cf. Fig. 163.

Remarks.—This species differs from *B. foliosa* by the morphology of the supravelar row of spines and the syllobial cusps; it is further decidedly smaller.

Occurrence.—Lower Visby Beds: Nyhamn, Gustavsvik (very rare).

Beyrichia (*Scabribeyrichia*) *foliosa* (Jones 1888)

Figs. 12, 164, and 165A.

1888 *Beyrichia tuberculata* var. *spicata* nov.—Jones 1888 a, p. 402; Pl. XXI, figs. 13 and 14.

1888 *Beyrichia tuberculata* var. *foliosa* nov.—Jones 1888 a, p. 403; Pl. XXI, figs. 15–17.

Type Reference.—Lectotype designated herein, p. 26.

Diagnosis.—Large *Beyrichia* (*Scabribeyrichia*) sp. with a swelling consisting of more or less fused tubercles in the region of the calcarine tubercle.

Description.—Only the cuspidal part of the anterior lobe is well set off as a lobal feature; its cusp is low and truncate. The anterior cusp of the syllobium is very high, cylindrical and more or less truncate; the posterior syllobial cusp is considerably suppressed. There is a somewhat constricted zygal arch, a syllobial groove, and often a distinct callus.

All the lobes, including their cusps, the velar ridge, and the crumina are tuberculate. The anteroventral part of the valve is comparatively finely tuberculate. The anterior part of the row of spines below the syllobial groove is greatly swollen, and a group of smaller spines or tubercles are often incorporated with this swelling. One spine, which is probably to be designated as the uncular spine, though it occupies an almost acroidal position, is very well developed; between this spine and the calcarine complex there are often only two large spines. Especially posteriorly on the velar ridge the tubercles tend to become prolongated into spines. There are a few characteristic tubercles dorsally above the adductorial sulcus.

Earlier moult stages show that the calcarine spine complex may be entirely dominated by a normal calcarine spine (Fig. 164C).

Dimensions.—Hinge length–sulcal height of a female specimen from Enholmen: 2615 μ – 1370 μ. The holotype, from Slite II: 2105 μ – 1380 μ.

Remarks.—For differential diagnostics, see under *B. hirsuta*, p. 300.

Occurrence.—Slite Beds: Enholmen, Slite II, Follingbo III.

Beyrichia (aff. *Scabribeyrichia*) sp.

Figs. 165B and C.

Remarks.—Within the subgenus *Scabribeyrichia* a reduction of the syllobial supravelar tuberculation has taken place; as suggested by Fig. 165A, showing a female specimen of *B. foliosa* with only a low swelling in the calcarine region, without any fusion of the tubercles there, this can probably take place within a species.

At Stora Myre (Slite Beds) two tecnomorphic specimens have been found (Fig. 165B and C) which agree with *Beyrichia* (*Scabribeyrichia*) as to the morphology of the syllobial cusps and even as to the tuberculation of the area near the hingeline above the adductorial sulcus. The morphology of the zygal

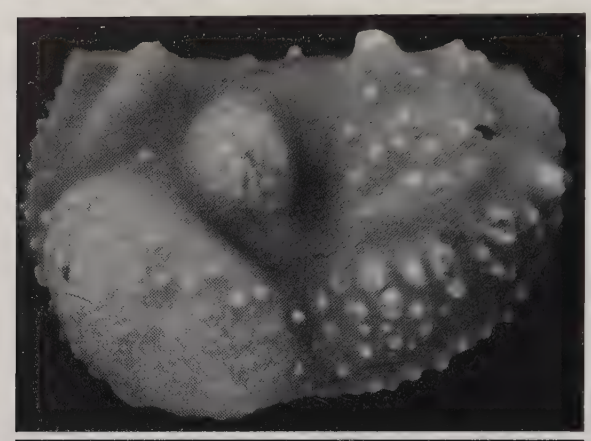


Fig. 165 A. *Beyrichia* (*Scabribeyrichia*) *foliosa* (Jones 1888). Female specimen without fusion of the tubercles in the calcarine region. Slite Beds, Enholmen. RM No. 25888:2. × 30.

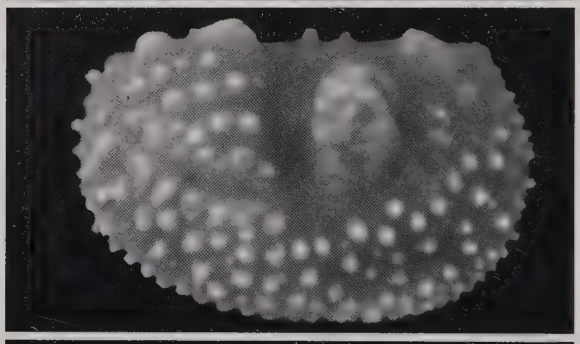


Fig. 165 B. *Beyrichia* (aff. *Scabribeyrichia*) sp., Slite Beds, Stora Myre. Tecnomorph, No. G 595. × 30.

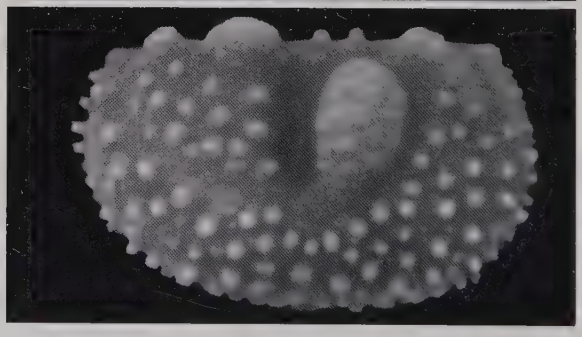


Fig. 165 C. Same species and locality. Tecnomorph, No. G 596. × 30.

and supravelar region are, however, quite different, and these forms are not covered by the subgeneric diagnosis. They are treated with open nomenclature here, as no adult female specimens could be obtained in spite of the very large size of the samples. They have, however, been considered as the males of the *Beyrichia erinacea*, but the females of this species are far from reaching the size and cuspidal morphology (cf., however, a certain cuspidal dimorphism in *B. hirsuta*) of these enigmatic tecnomorphs.

Dimensions.—Hinge length–sulcal height in the material from Stora Myre: 1815 μ – 1300 μ, 1795 μ – 1225 μ.

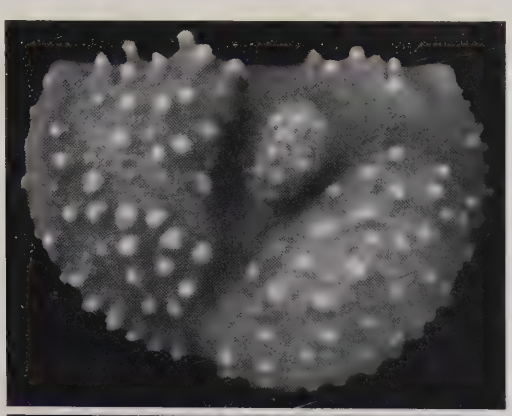


Fig. 166 A. *Beyrichia* (*incerti subgeneris*) *erinacea* n.sp., Slite Beds, Stora Myre. Female, No. G 597 (holotype). ×40.

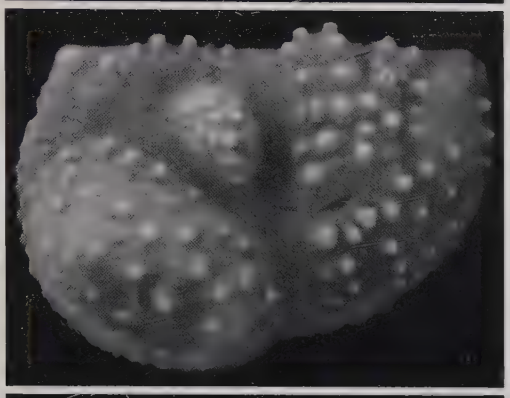


Fig. 166 B. Same species and locality. Female, No. G 598. ×40.

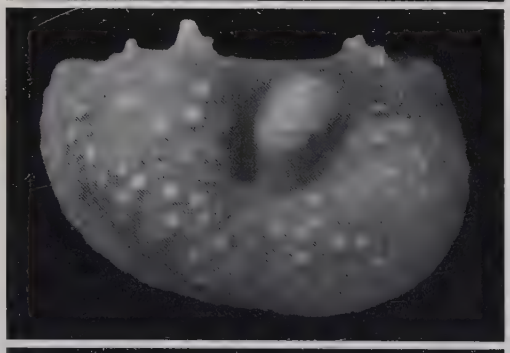


Fig. 166 C. *Beyrichia* (*Asperibeyrichia*) *haidbeynsis* n.sp., Hemse Beds, Haidby. Female, RM No. Ar 25950:2. ×40

Fig. 166 D. Same species and locality. Young tecnomorph, RM No. Ar 25949:1. ×40.

Beyrichia (*incerti subgeneris*) *erinacea* n.sp.

Figs. 166A–B.

Derivation of the Name.—Latinized Greek *erinacea*, a (female) hedgehog, alluding to the spinosity of the species.

Holotype.—A right female valve, No. G 597 (Fig. 166A).

Type Stratum and Type Locality.—Slite Beds at Stora Myre, Gotland.

Diagnosis.—Small *Beyrichia* species without marked lobal cusps; lobes finely spinose without other differentiations than a very shallow syllobial groove; crumina very large and tuberculate.

Description.—Only female specimens known. The anterior lobe is marked only as a low, spinose ridge in its cuspidal part. The syllobium is also finely spinose and not markedly set off from the velar ridge; the relatively small preadductorial knob is tuberculate, even with some tendency to spinosity. The crumina has a markedly anterior position and is the most voluminous extension of the valve.

Dimensions.—Hinge length–sulcal height of female specimens from Stora Myre, in microns: 1485–1030, 1480–1010, 1410–1025, 1410–985, 1380–1100.

Remarks.—No species invites a systematic comparison, and, although 16 adult females are known, it has not been possible to identify any tecnomorphs. As mentioned above attempts have been made to correlate these females with the two tecnomorphs described above. In order to do this, however, we have to premise larger dimorphic lobal modifications than known in any other species and also premise that the differences in linear dimensions depend on the relatively large part of the increase in volume needed for the crumina. This explanation is not impossible, though it is still inexplicable why the hundreds of small tecnomorphs to be expected have not been found.

Occurrence.—Slite Beds: Stora Myre.

Subgenus *Beyrichia* (*Asperibeyrichia*) n. subg.

Fig. 167.

Derivation of the Name.—Latin *asper*, rough, alluding to the spinosity of especially the cuspidal parts of the lobes.

Types Species.—*Beyrichia* (*Asperibeyrichia*) *hystricoides* n.sp.

Species.—*Beyrichia* (*Asperibeyrichia*) *hystricoides* n.sp.
Beyrichia (*Asperibeyrichia*) *haidbyensis* n.sp.
Kloedenia apiculata Jones 1888

Diagnosis.—*Beyrichia* species in which the crumina is an anterior swelling of the carapace, without any distinct limitation towards the lobal parts. There are remains of a zygal arch.

Beyrichia (*Asperibeyrichia*) *hystricoides* n.sp.

Figs. 168 and 169.

Derivation of the Name.—Latinized Greek *hystricoides*, similar to a porcupine, alluding to the dorsal spinosity.

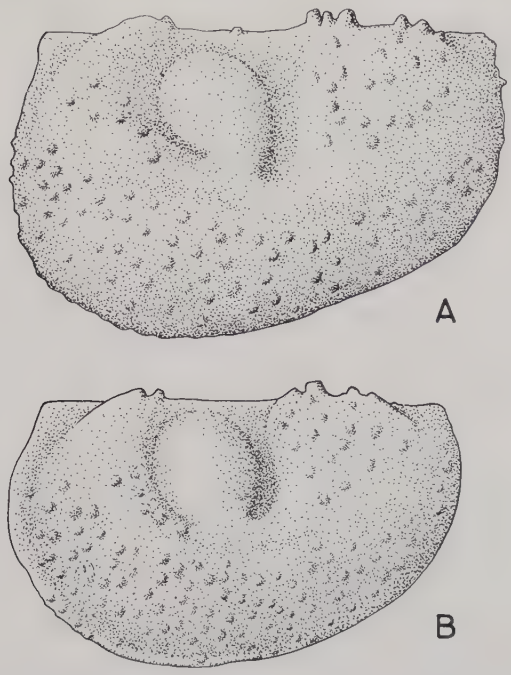


Fig. 167. *Beyrichia* (*Asperibeyrichia*) n.subg. Drawing based on specimens of *Beyrichia* (*Asperibeyrichia*) *hystricoides* n.sp. ×40. A. Female. B. Male.

Holotype.—A left female valve, No. G 601 (Fig. 169 A).

Type Stratum and Type Locality.—Högklint Beds at Lickershamn II, Gotland.

Diagnosis.—*Beyrichia* (*Asperibeyrichia*) species without very pronounced spinosity on the anterior lobe and with a lobule between the crumina and the preadductorial knob.

Description.—The protruding cusp of the anterior lobe shows a normal beyrichiid development, but the syllobial cusps are covered and almost hidden by small spines. The sulci and the preadductorial knob are the only very marked features; the other parts of the lobes are fused and slope gently down towards the low velar ridge. The prenodal sulcus is very narrow; the inflation of the crumina causes an extra lobule bounded by this sulcus and a very shallow sulcule. There is a short zygal ridge in both sexes and a shallow syllobial groove below and behind it. The tuberculation is almost undifferentiated, except for a row below the syllobial groove which tends to grow out into spines, and for the cuspidal spines mentioned. A few tubercles sometimes occur above the adductorial sulcus.

Dimensions.—Hinge length–sulcal height of female specimens, in microns: From Lickershamn II (Högklint Beds): 1930 ca. 1265, 1815–1250. From Bingers (Tofta Beds): 1630–1030, 1465–1000, 1400–865.

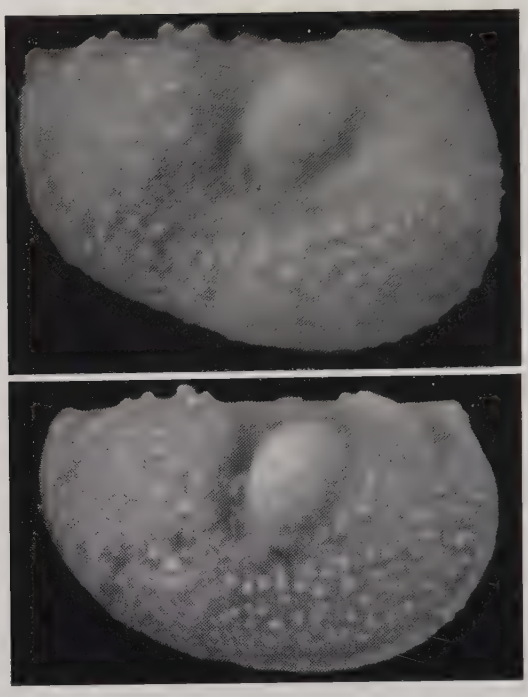


Fig. 168 A. *Beyrichia* (*Asperibeyrichia*) *hystricoides* n.sp., Tofta Beds, Bingers. Female valve, No. G 599. ×40.

Fig. 168 B. Same species and locality. Male valve, No. G 600. ×40.

Remarks.—The material from the Tofta Beds varies towards an almost complete obsoletion of the spinosity; however, it is difficult to judge to what extent this is due to a secondary destruction of the valves. The difference in dimensions of this material as compared with topotype material is also considerable; the supracruminal lobule is always lower.

This species differs from *B. haidbyensis* by its cuspidal morphology and the presence of the supracruminal lobule.

Occurrence.—Högklint Beds: Lickershamn II. Tofta Beds: Galgberget, Bingers.

Beyrichia (*Asperibeyrichia*) *haidbyensis* n.sp.

Figs. 166C–D.

Derivation of the Name.—Latin *Haidbyensis*, from Haidby in the parish of Kräklingbo, Gotland.

Holotype.—A right female valve, RM No. Ar 25950: 2 (Fig. 166C).

Type Stratum and Type Locality.—Hemse Beds at Haidby, Gotland.

Diagnosis.—*Beyrichia* (*Asperibeyrichia*) species with high tubercles or small spines also on the anterior lobe and with all three lobal cusps drawn out into spines. There is no distinct lobule between the crumina and the preadductorial knob.

Description.—The adductorial sulcus is well marked; the prenodal sulcus

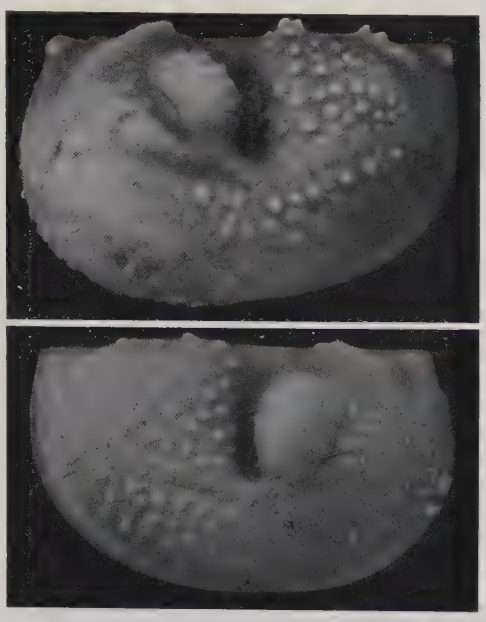


Fig. 169 A. *Beyrichia* (*Asperibeyrichia*) *hystricoides* n.sp. Högklint Beds, Lickershamn II. Female valve, No. G 601 (holotype). ×30.

Fig. 169 B. Same species and locality. Male valve, No. G 602. ×30.

is very shallow. The zygal arch is distinct at least in the tecnomorphs, and there is a very shallow syllobial groove. The tuberculation, except on the lobal cusps, is not much differentiated, but there is a tendency towards an enlargement of the tubercles forming a row below the syllobial groove.

The lobal cusps are prolonged into spines; the spine formed on the posterior syllobial groove is fairly small.

Dimensions.—Hinge length of the holotype 1290 μ, height over the adductorial sulcus 865 μ.

Occurrence.—Hemse Beds: Haidby.

Beyrichia (*Asperibeyrichia*) *apiculata* (Jones 1888)

Figs. 11 A–D.

1888 *Kloedenia apiculata* sp. nov.—Jones 1888 a, p. 398; Pl. XXI, figs. 1–5.

Type Reference.—Lectotype designated herein, p. 25.

Diagnosis.—*Beyrichia* (*Asperibeyrichia*) species with only one, pointed syllobial cusp and without spines on the lobal cusps. There is no lobule between the crumina and the preadductorial knob.

Description.—The syllobial cusp and the cusp of the anterior lobe are pointed or only very slightly truncate, protruding considerably over the hingeline. The remains of the zygal arch are inconsiderable; there is an almost complete constriction of the zygal connection near the anterior end of the distinct syllobial groove. The preadductorial knob is rounded and strongly protruding; the adductorial sulcus behind it is strongly marked and deep; the prenodal sulcus

is short and shallow. The velum is reduced to a bend. The ornamentation is an undifferentiated fine tuberculation on the lobes; the crumina is smooth.

Dimensions.—Hinge length of the lectotype (extrapolation) ca. 2030 μ, height over the adductorial sulcus 1345 μ.

Remarks.—This species differs considerably from the two other species in the subgenus by the morphology of the lobal cusps and the zygal region, and by its finer tuberculation and lack of spinosity.

Occurrence.—Slite Beds: Norrbys, Follingbo III, Kyllej, Enholmen, Slite II.

Subgenus Beyrichia (*Simplicibeyrichia*) n. subg.

Fig. 140 C.

Derivation of the Name.—Latin *simplex*, simple, and the generic name *Beyrichia*, referring to the simple arrangement of the anterior lobe, the cuspidal part of the syllobium, and the ornamentation in general.

Type Species.—*Beyrichia* (*Simplicibeyrichia*) *globifera* n.sp.

Species.—*Beyrichia* (*Simplicibeyrichia*) *impersonalis* n.sp.
Beyrichia (*Simplicibeyrichia*) *globifera* n.sp.
Beyrichia (*Simplicibeyrichia*) *callifera* n.sp.
Beyrichia (*Simplicibeyrichia*) *duplicicalcarata* n.sp.
Beyrichia (*Simplicibeyrichia*) *barbulimentata* n.sp.

Diagnosis.—*Beyrichia* species with a short adductorial sulcus and a distinct, low syllobial groove but nevertheless with no tendency to form a zygal arch. One low syllobial cusp or none at all. There are marked trends towards the obsoletion of the prenodal sulcus and the development of a calcarine spine.

Beyrichia (*Simplicibeyrichia*) *impersonalis* n.sp.

Fig. 170.

Derivation of the Name.—Latin *impersonalis*, referring to the poor development of sulcal and ornamental features.

Holotype.—A left female valve, No. G 603 (Fig. 170A).

Type Stratum and Type Locality.—Hemse Beds at Fakle, Gotland.

Diagnosis.—Large *Beyrichia* (*Simplicibeyrichia*) species without a calcarine spine. The syllobial cusp is more or less developed as a ridge; the prenodal sulcus is almost obsolete. The velar outline is sharply curved posteroventrally.

Description.—Few features can be added. There is a syllobial groove without a marked callus. The prenodal sulcus is more distinct in the only female specimen known, and the preadductorial knob is less displaced by the crumina than in the other species of this subgenus. The ornamentation probably consisted of a granulosity which has been destroyed in the extant material, a very slight verrucosity on the syllobium, and some anteroventral velar tubercles.

Dimensions.—Hinge length of the holotype 2275 μ, height over the adductorial sulcus 1445 μ.

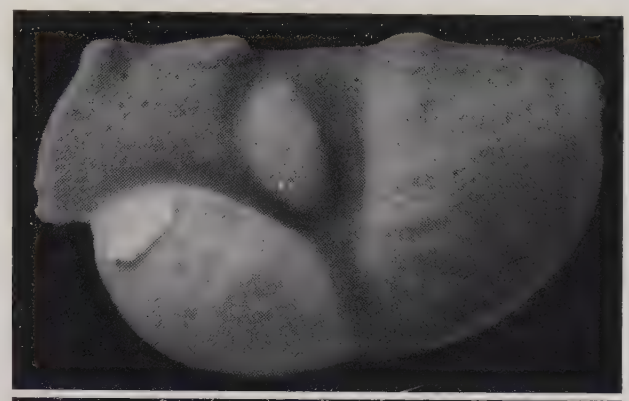


Fig. 170 A. *Beyrichia* (*Simplicibeyrichia*) *impersonalis* n.sp., Hemse Beds, Fakle. Female valve, No. G 603 (holotype). ×30.

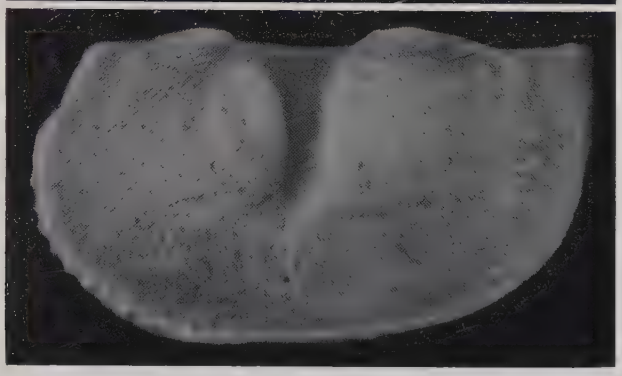


Fig. 170 B. Same species and locality. Male carapace, No. G 604. ×30

Remarks.—This species is closely related to *B. globifera* but differs from it by its much larger size, the sharp posteroventral curve of the velar outline, and, as far as this can be established from the extant material, by the absence of a calcarine tubercle or spine.

Occurrence.—Hemse Beds: Fakle.

Beyrichia (*Simplicibeyrichia*) *globifera* n.sp.

Figs. 9B, 40C and D, 171, 172, and 176B.

1888 *Beyrichia Klödeni* var. *protuberans* Boll—Kiesow, Pl. I, fig. 5.

Derivation of the Name.—Latin *globifer*, carrying a globe, referring to the shape of the crumina.

Holotype.—A left female valve, No. G 606 (Fig. 171B).

Type Stratum and Type Locality.—Hemse Beds at Hammarudden, Gotland.

Diagnosis.—Normally preplete *Beyrichia* (*Simplicibeyrichia*) species with a low syllobial cusp, developing a fine calcarine tubercle or spine. The syllobial groove is very shallow or obsolete, always without a callus.

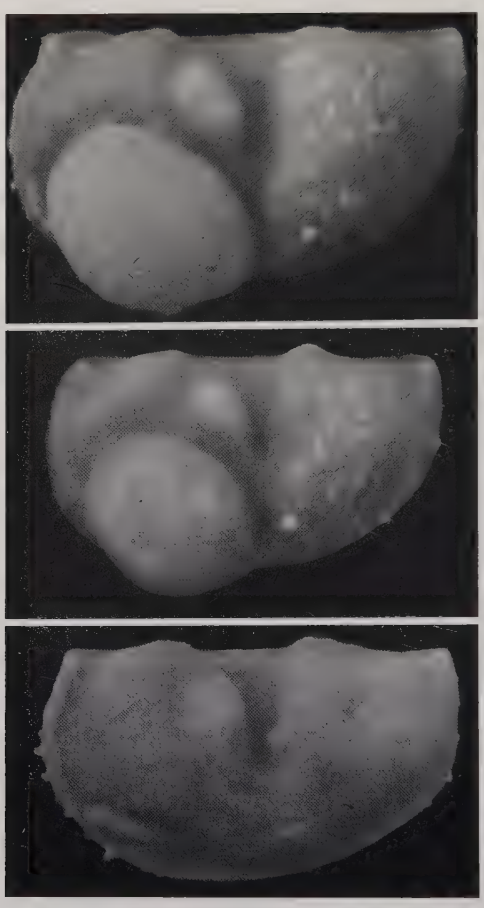


Fig. 171 A. *Beyrichia* (*Simplicibeyrichia*) *globifera* n.sp., Hemse Beds, Sigvalde. Female valve, No. G 605. × 30.

Fig. 171 B. Same species, Hemse Beds, Hammarudden. Female valve, holotype, No. G 606. × 30.

Fig. 171 C. Same species. Hemse Beds, Hammarudden. Tecnomorph, No. G 607. × 30.

Description.—The low lobal cusps usually protrude distinctly but only slightly over the hingeline. In the tecnomorphs the preadductorial node is almost fused with the flattened anterior lobal area. The low velar ridge is set off from the lobal area of the valve. The crumina is conspicuously globular. The syllobium is ornamented with a low verrucosity which does not completely break through the granulosity of the surface. There is, at least in the females, a calcarine tubercle or spine. Velum sparsely tuberculate.

Dimensions.—Hinge length–sulcal height of female valves, in microns:

From Sigvalde: 1845–1130, 1845–1165. From Lau Backar: 1810–1230, 1795–1220.

Remarks.—This species differs from *B. impersonalis* as stated under this species and from *B. callifera* and *B. duplicicalcarata* by the outline of the valve the shape of the crumina, the morphology of the cuspidal parts of the lobes, and by the absence of a callus. It has the same prepletion of the outline as *B.*

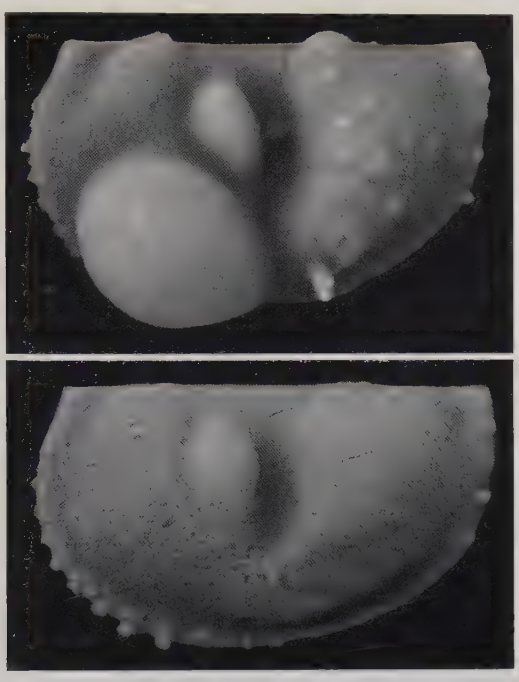


Fig. 172 A. *Beyrichia* (*Simplicibeyrichia*) *globifera* n.sp., Eke Beds, Lau Backar. Female valve, No. G 608. × 30.

Fig. 172 B. Same species and locality. Tecnomorph, No. G 609. × 30.

barbulimentata but differs from it by the lack of a spinose ornamentation and a callus.

Occurrence.—Hemse Beds: Hammarudden, Grogarns, Hammars, Gannes, Fakle, Haidby, Sigvalde, Tänglings. Eke Beds: Lau Backar.

Beyrichia (*Simplicibeyrichia*) *callifera* n.sp.

Figs. 173 A and B.

Derivation of the Name.—Latin *callifer*, bearing a callus, alluding to this structure as the most conspicuous ornamental feature in this species.

Holotype.—A left female valve, RM No. Ar 25950: 1 (Fig. 173 A).

Type Stratum and Type Locality.—Hemse Beds at Haidby, Gotland.

Diagnosis.—Small tuberculate or verrucose, subamplete *Beyrichia* (*Simplicibeyrichia*) species with a large crumina, a thick callus in the female and a thin one in the tecnomorphs. Calcarine tubercle poorly developed.

Description.—There are no lobal cusps. The crumina is very large and longish with a strongly inclined axis. The velum is a low ridge, very distinctly set off from the lobal parts of the valve; it is sparsely tuberculate.

Dimensions.—Hinge length of the holotype 1370 μ, height over the adductorial sulcus 960 μ.

Remarks.—This species is very similar to *B. duplicicalcarata* but differs from it by the ornamentation and the morphology of the callus and the calcarine region.

Occurrence.—Hemse Beds: Haidby.

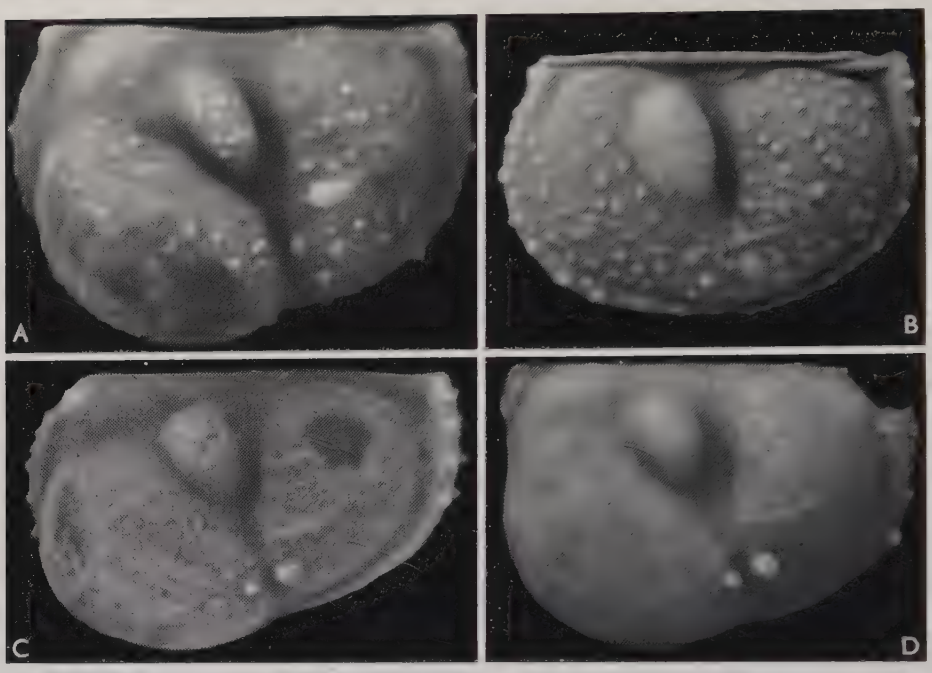


Fig. 173. A–B. *Beyrichia* (*Simplicibeyrichia*) *callifera* n.sp., Hemse Beds, Haidby. ×40. A. Female, RM No. Ar 25950:1 (holotype). B. Tecnomorph, RM No. 25949:2. C–D. *Beyrichia* (*Simplicibeyrichia*) *duplicicalcarata* n.sp., Eke Beds, Lau Backar. ×40. C. Female, No. G 612 (holotype). D. Female, No. G 613.

Beyrichia (*Simplicibeyrichia*) *duplicicalcarata* n.sp.

Figs. 173 C and D.

Derivation of the Name.—Latin *duplex*, double, and *calcaratus*, provided with spurs, alluding to the characteristic arrangement with a small extra spur on the crumina.

Holotype.—A female carapace, No. G 612 (Fig. 173 C).

Type Stratum and Type Locality.—Eke Beds at Lau Backar, Gotland.

Diagnosis.—Small *Beyrichia* (*Simplicibeyrichia*) species with a very large crumina without lobal ornamentation and cusps. In front of the calcarine spine there is a similar tubercle or spine on the posterior part of the crumina.

Description.—The crumina is even larger than in *B. callifera*; the incorporation of wall elements approaches the anterior cardinal corner. The syllobial callus is thin in the female also, and there is no discernible groove below it. The velum is well set off from the lobal parts of the valve; in the female it is sparsely tuberculate anteriorly and posteriorly.

Dimensions.—Hinge length–sulcal height of two female specimens from Lau Backar: 1345 μ – 960 μ, 1185 μ – 830 μ.

Remarks.—The tecnomorphs have not been identified—probably because

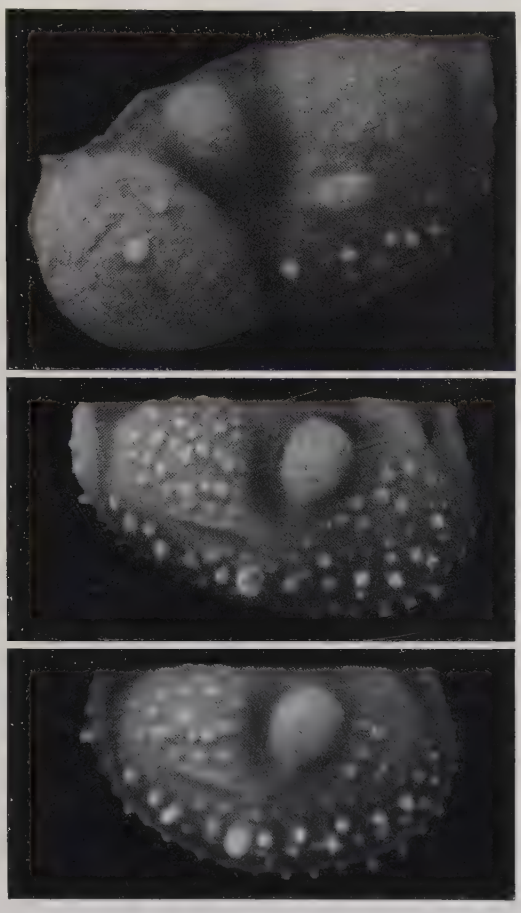


Fig. 174 A. *Beyrichia* (*Simplicibeyrichia*) *barbulimentata* n.sp., Hamra Beds, Hoburgen II a. Fragmentary female valve, No. G 614. ×30.

Fig. 174 B. Same species, Hamra Beds, Hoburgen II b. Tecnomorphic valve, No. G 615 (holotype). ×30.

Fig. 174 C. Same species, Hamra Beds, Hoburgen IIa. Tecnomorphic valve, No. G 616. ×30.

of the difficulty in finding them among the abundant small tecnomorphs of *B. globifera*—and it is, therefore, not known how the calcarine tubercles are developed in the other sex or whether the callus shows the same dimorphic trends as in the preceding and the following species.

Occurrence.—Eke Beds: Lau Backar (very rare).

Beyrichia (*Simplicibeyrichia*) *barbulimentata* n.sp.

Fig. 174.

Derivation of the Name.—A diminutive of Latin *barba*, beard, and *mentatus*, having a chin, alluding to the short spinosity on the flattened lower part of the anterior lobe.

Holotype.—A right tecnomorphic valve, No. G 615 (Fig. 174B).

Type Stratum and Type Locality.—Hamra Beds at Hoburgen IIb, Gotland.

Diagnosis.—Longish, preplete *Beyrichia* (*Simplicibeyrichia*) species with a

well isolated preadductorial knob, a distinct syllobial groove with a thin callus in the tecnomorphs, and a short, thick callus without a groove in the female. Cuspidal parts of the lobes rounded; valves verrucose laterodorsally and spinose lateroventrally; there is a prominent calcarine spine.

Description.—The cuspidal parts of the lobes protrude only slightly over the hingeline. The part of the syllobium above the syllobial groove or callus is coarsely verrucose in the tecnomorphs; in the only female specimen known the verrucosity does not completely break through the granulosity. The other lobal parts of the valve, except for the cuspidal part of the anterior lobe, are coarsely tuberculate or finely spinose; anteriorly the spinosity is limited by a tuberculate-verrucose zone. The velum is a distinct ridge with sparse spines or tubercles along all its length.

Remarks.—This species has the general carapace shape of *B. globifera*, but shows the same development of the syllobial groove and callus as the subamplete *B. callifera* which further differs from it by having a much larger crumina. *B. barbulimentata* is further the only species in the subgenus with a spinulose lobal ornamentation.

Occurrence.—Hamra Beds: Gisle, Hoburgen IIa, Hoburgen IIb. The species also occurs in a new sample (1961) from the basal Hamra Beds below Hoburgen IIa. Sundre Beds: Juves.

Subgenus *Beyrichia* (*Lunulibeyrichia*) n. subg.

Derivation of the Name.—Diminutive of Latin *luna*, the moon, referring to the long, crescent-shaped carapace.

Type Species.—*Beyrichia* (*Lunulibeyrichia*) *birupta* n.sp.

Species.—Only the type species.

Diagnosis.—Long *Beyrichia* species with a broad bicuspidate syllobium, wide and distinctly marked velar ridge, a well marked anteroventral depression, and a lower depression in the lobal connection above it. There is no pronounced trend towards a connection between the prenodal sulcus and the anteroventral depression.

Remarks.—In several respects, such as the carapace shape, the wide velar ridge, the presence of an unusually distinct anteroventral depression, and a ventral widening of the anterior lobe, this subgenus is similar to *Neobeyrichia*. It differs from this genus by the cuspidal morphology and by the fact that the lobal connection below the preadductorial node is not broken by any incisions from the prenodal sulcus or the anteroventral depression.

Beyrichia (*Lunulibeyrichia*) *birupta* n.sp.

Fig. 175.

Derivation of the Name.—Latin *bis*, twice, and *ruptus* (from *rumpere*), broken, alluding to the two bends in the posteroventral outline of the female velum.

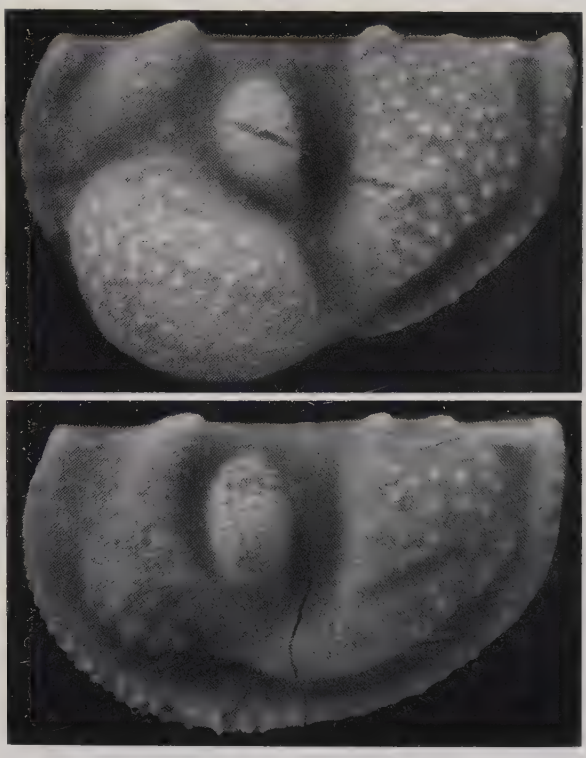


Fig. 175 A. *Beyrichia* (*Lunulibeyrichia*) *birupta* n.sp., Slite Beds, Follingbo I. Female valve, No. G 610 (holotype). × 30.

Fig. 175 B. Same species and locality. Male valve, No. G 611. × 30.

Holotype.—A left female valve, No. G 610 (Fig. 175 A).

Type Stratum and Type Locality.—Slite Beds at Follingbo I, Gotland.

Diagnosis.—As for the subgenus.

Description.—All lobal cusps protrude slightly over the hingeline. The anterior lobe widens ventrally. The preadductorial knob is widely connected with the lobal parts below it in the tecnomorph; there is a shallow syllobial groove without a callus.

The broad velar ridge is fairly abruptly bent posteroventrally; owing to the constriction of the velum behind the crumina there is one more, similar bend in the velar outline of the female; even in the male the straight ventral outline ends with a slight bend posteroventrally.

All the lobal features and the crumina are about equally verrucose; the velar edge is tuberculate, with the densest tuberculation anteroventrally.

Dimensions.—Hinge length–sulcal height of female specimens from Follingbo I, in microns: 2780–1625, 2695–1545, 2650–1545, 2539–1480, 2500–1545.

Occurrence.—Slite Beds: Norrbys, Follingbo I, Follingbo II, Follingbo III.

Genus *Neobeyrichia* Henningsmoen 1954

Figs. 140C–D.

Type Species.—*Beyrichia Buchiana* Jones 1855 (cf. Henningsmoen 1954, p. 25; cf. Fig. 2A in the present paper).

Subgenera.—*Neobeyrichia* (*Neobeyrichia*) Henningsmoen 1954
Neobeyrichia (*Nodibeyrichia*) Henningsmoen 1954

Diagnosis.—*Beyrichiinae* with one syllobial cusp, lacking uncular and calcarine spines and a velar edge on the crumina. The anterior lobe is isolated or almost isolated by a connection of the prenodal sulcus with the anteroventral depression.

Restriction of the Genus.—As defined by Henningsmoen (1954, p. 25) the genus comprises different beyrichiids with an isolated anterior lobe. However, there are similar trends towards isolating the anterior lobe in both the subfamilies *Amphitoxotidinae* and *Beyrichiinae* which has had as a consequence that species belonging to the present genera *Sleia*, *Hemsiella*, and *Macrypsilon* were included in *Neobeyrichia* (and not in *Velibeyrichia* or *Dibolbina* which were then the only existing supraspecific taxia among the *Amphitoxotidinae*). These forms are, consequently, excluded from the genus here.

Though not constituting as sharp a boundary as suggested by old beyrichiid illustrations, the isolation of the anterior lobe must be retained as the main diagnostics in comparison with *Beyrichia*, as introduced by Henningsmoen (op. cit.). On the other hand, it will be shown that the transition towards forms represented by the type species of *Nodibeyrichia*, i.e. *Beyrichia Bronni* Reuter 1885, is very gradual; this means as far as lobulate forms without long spines on the lobes are concerned. It is still possible to retain a restricted *Nodibeyrichia*, and then as a subgenus of *Neobeyrichia*.

The closely interrelated lobulate forms with acroidal, uncular, and calcarine spines constitute a homogeneous group which would be cut into widely separated parts by generic boundaries mechanically based on the isolation of an anterior lobe and the dissection of the lobes into lobules. They are separated as constituting the genus *Calcaribeyrichia* in which the anteroventral morphology varies between a simple lobal connection of *Beyrichia* type and an advanced lobulation of *Nodibeyrichia* type; this genus is kept together by a characteristic lobulation of the syllobium, coupled with the development of long spines on the syllobium. This means, again, a restriction of *Neobeyrichia*. The morphological trends in *Calcaribeyrichia* are also found in *Plicibeyrichia* and *Gannibeyrichia* which contain only new species.

Subgenus *Neobeyrichia* (*Neobeyrichia*) Henningsmoen 1954

Fig. 140C.

Type Species.—*Beyrichia Buchiana* Jones 1855.

Species.—*Neobeyrichia* (*Neobeyrichia*) *ctenophora* n.sp.

Beyrichia Lauensis KIESOW 1888
Beyrichia Buchiana JONES 1855
Beyrichia Buchiana var. *nutans* KIESOW 1888
Beyrichia spinulosa BOLL 1856 (syn. *B. nodulosa* BOLL 1862)
Beyrichia Lindströmi var. *expansa* KIESOW 1888

DIAGNOSIS.—*Neobeyrichia* species without lobular differentiation of the anterior lobe.

Neobeyrichia (*Neobeyrichia*) *ctenophora* n.sp.

Fig. 176 A and C.

1888 *Beyrichia Klödeni* var. *protuberans* BOLL—KIESOW, Pl. II, figs. 4a–c (cf. Fig. 9A herein).

DERIVATION OF THE NAME.—Latinized Greek *ctenophorus*, bearing a comb, alluding to the spinosity on the anteroventral part of the velum.

HOLOTYPE.—A left female valve, No. G 617 (Fig. 176A).

TYPE STRATUM AND TYPE LOCALITY.—Eke Beds at Lau Backar, Gotland.

DIAGNOSIS.—Large, longish *Neobeyrichia* (*Neobeyrichia*) species with a broad, undissected syllobium and a not completely isolated anterior lobe, narrowly connected with the other lobes between the sharply incised prenodal sulcus and the anteroventral depression.

DESCRIPTION.—The anterior lobe is broadly crescent-shaped with a pointed cusp. The preadductorial knob is longish and has a low connection with the syllobium. The syllobial cusp is small, markedly set off from the syllobium. The syllobial groove, if discernible at all, is very shallow; there is no callus.

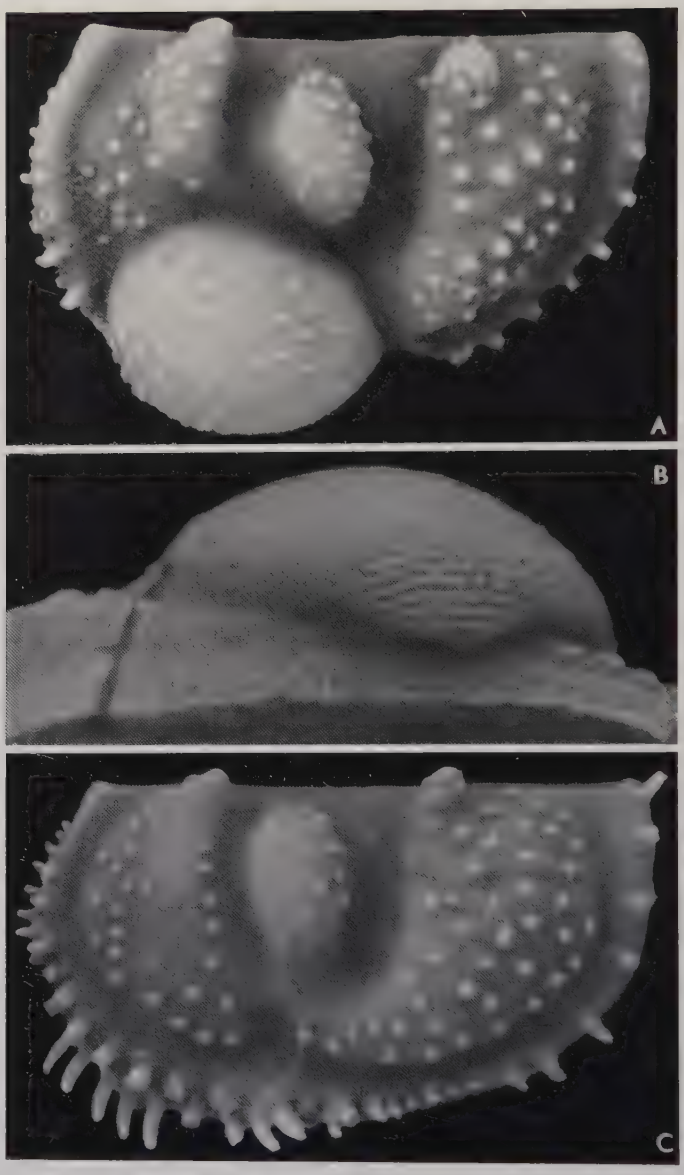
The velum is a broad ridge, markedly set off from the lobal parts of the valve. The crumina has the normal beyrichiine field with a finger-print striation; this part of the crumina does not show reductions of the kind found in *Beyrichia* (*Simplicibeyrichia*) (Fig. 176 B) and *Beyrichia* (*Asperibeyrichia*).

All lobal parts and the crumina have a low tuberculation; the velum is strongly spinose, especially anteroventrally.

DIMENSIONS.—Hinge length–sulcal height of female specimens from Lau Backar: 2695 μ – 1575 μ, 2660 μ – 1615 μ, 2630 μ – 1450 μ.

REMARKS:—This species must be regarded as a primitive representative of the genus; in the other species the development towards slenderness of the lobes and dissection of the syllobium has proceded further. The dense spinosity of the velum is another absolutely distinctive character which is primitive.

OCCURRENCE.—Hemse Beds: Lukse (!), Tjängdarve, Medbys. Eke Beds: Lau Backar, Halor, Eke, Herrvide, Petsarve, Lingvide, Ronnings. Burgsvik Beds: Husryggen. Hamra Beds: Lunde, Hoburgen Ia, Hoburgen IIa, Sundre Beds: Juves.



Neobeyrichia (*Neobeyrichia*) *ctenophora* n.sp. Female, No. G 617 (holotype). × 30.

Beyrichia (*Simplicibeyrichia*) *globifera* n. sp. Crumina in ventral view, anterior end to the right, No. G 618. × 60.

Neobeyrichia (*Neobeyrichia*) *ctenophora* n.sp. Male, No. G 619. × 30.

Fig. 176. *Neobeyrichia* (*Neobeyrichia*) *ctenophora* n.sp. and *Beyrichia* (*Simplicibeyrichia*) *globifera* n.sp. Eke Beds, Lau Backar.

Neobeyrichia (*Neobeyrichia*) *lauensis* (KIESOW 1888)

Figs. 10, 177, and 178.

1888 *Beyrichia Lauensis* nov. sp.—KIESOW, p. 8; Pl. II, figs. 1 and 2.

NEOTYPE.—The search for those of KIESOW's originals which were not deposited in Stockholm has hitherto been in vain (cf. p. 29). A specimen which

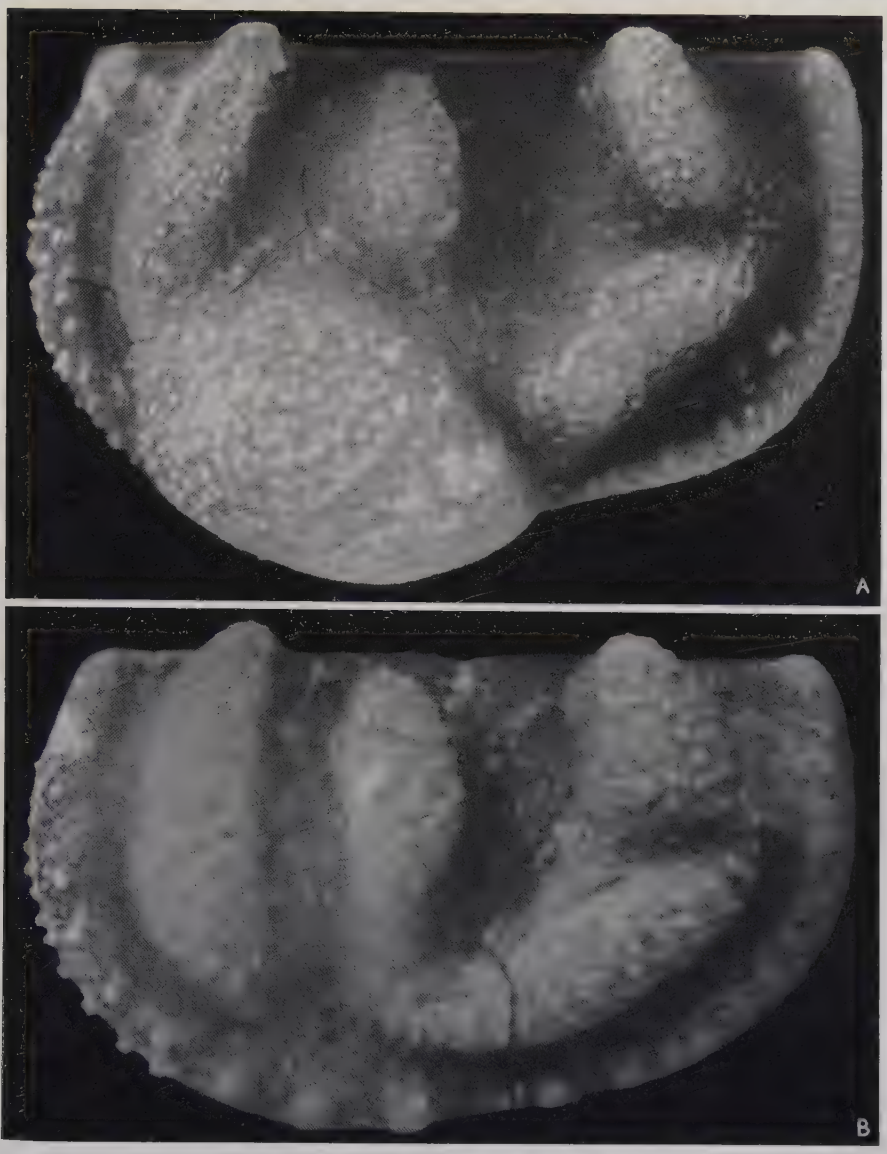


Fig. 177. *Neobeyrichia* (*Neobeyrichia*) *lauensis* (KIESOW 1888), Hemse Beds, Hulte. A. Female carapace, No. G 622 ×25. B. Tecnomorphic valve, No. G 623. ×30.

can possibly be identified as autohyle has been figured here (Fig. 10A). There are a few ostracode specimens in KRAUSE's collections in Berlin which seem to have been collected along KIESOW's route on Gotland, but it cannot be proved by whom. The material of *N. lauensis* is from Burs, not from Lau, and even if the *intentio auctoris* can be illustrated by the fact that the specimen in Fig. 10

Fig. 178. *Neobeyrichia* (*Neobeyrichia*) *lauensis* (Kiesow 1888), Hemse Beds, Hulte. Female carapace in ventral view (anterior end up), No. G 622 (same as Fig. 177 A). × 25.

has at least been owned by a contemporary specialist in the author's environment this is not formally sufficient for a type selection.

As neotype a left tecnomorphic valve, No. G 621, from the uppermost Hemse Beds at Botvide in the parish of Lau, Gotland, is selected here.

Diagnosis.—Extremely large *Neobeyrichia* (*Neobeyrichia*) species with a deep sulcule which divides the slender syllobium into two lobules.

Description.—All lobes slender; the anterior lobe is completely isolated from the others. The long preadductorial lobe is connected with the lower part of the syllobium by a low ridge. The lower syllobial lobule is about 1.5 times as long as the upper lobule, subparallel to the velum and forming an angle with the upper lobule of only a little more than 90°.

The velum is a broad, thick ridge, tuberculate with a row of very large tubercles anteroventrally and small tubercles or spines anteriorly. The lobes are granulose and finely tuberculate.

The crumina is not sharply constricted proximally. Laterally, it is tuberculate

like the lobes; its ventral ornamentation is best described as tuberculo-striate. Its inner base is finely striate.

There is a low toric ridge along the inner base of the velum. The vertical marginal structures are only low ridges; the covering structure is broad and finely tubulous, and the ends of the tubules are thickened, forming a fine edge crest.

Dimension.—Hinge length–sulcal height of two female specimens from Botvide: 4025 μ – 2695 μ, 3860 μ – 2595 μ. One female specimen from Hulte: 4050 μ – 2650 μ. This is the largest beyrichiid described.

Remarks.—*N. lauensis* is probably more closely related to the type species, *N. buchiana*, than any other species known but differs from it by its extreme size and by the deep syllobial sulcule.

Occurrence.—Hemse Beds: Gogs, Botvide, Gannor, Fie, Hägvide, Gläves, Vanges, Hulte, Tjängdarve, Linde, Amlings. Eke Beds: Ronnings.

Neobeyrichia (*Neobeyrichia*) *nutans* (Kiesow 1888)

Figs. 40B and 179.

1888 *Beyrichia Buchiana* var. *nutans* mihi—Kiesow, p. 7; Pl. I, figs. 11–14.

Neotype.—Kiesow's (1888, Pl. I, figs. 11–14) originals of this species have not been traced. There is only one species in the Östergarn region which can be identical with Kiesow's Pl. I, fig. 14. It is further known from a small rock sample in the State Museum of Natural History, No. Ar 25693, labelled "Kanalen från Visne myr" that the same species occurs in Fardhem together with *Hammariella pulchrivelata*, a species also characteristic of the shale exposed along the shore from Hammarudden to Skåne.

As neotype a left tecnomorphic valve is selected here, No. G 625 (Fig. 179B) from the Hemse Beds at Hammarudden (in the sense of the code name used in this paper) in the parish of Östergarn, Gotland.

Diagnosis.—Medium-sized *Neobeyrichia* (*Neobeyrichia*) species with an almost completely isolated anterior lobe. There is a low elevation separating the main part of the prenodal sulcus from the anteroventral depression. Syllobium with two shallow sulcular depressions, one of them in the region of the syllobial groove, the other subparallel to it and separating the cuspidal part of the syllobium.

Description.—Outline pronouncedly preplete; the prepletion is not mainly caused by a forward swing of the anterior part of the ventral margin but by the tapering of the posterior part of the outline. The lobal cusps protrude considerably over the hingeline and are of about equal size. There is an arched connection between the longish preadductorial knob and the slender syllobium. The velar flange is well marked; there is a wing-like extension of it in the postcruminate velar portion of the female, traced also in the male as a marked bend.

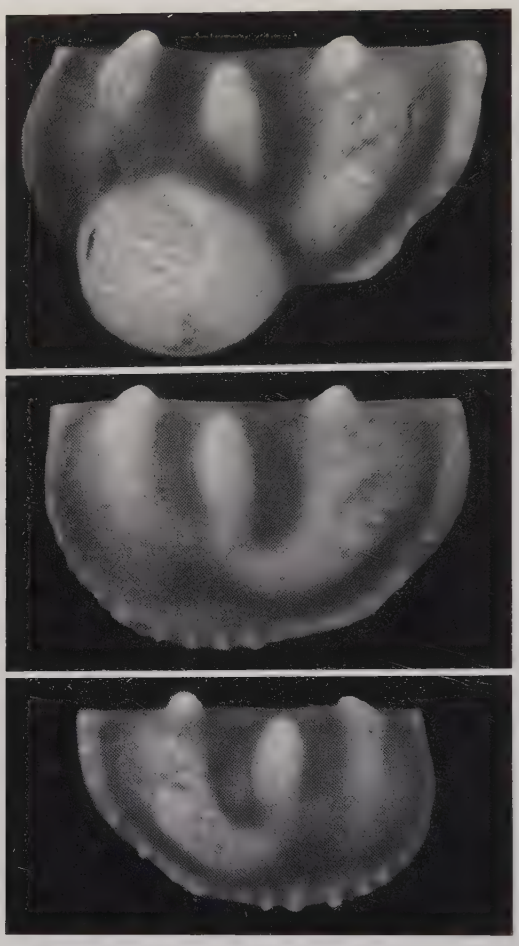


Fig. 179 A. *Neobeyrichia* (*Neobeyrichia*) *nutans* (Kiesow 1888), Hemse Beds, Hammarudden. Female, No. G 624. × 30.

Fig. 179 B. Same species and locality. Tecnomorph, No. G 625 (neotype). × 30.

Fig. 179 C. Same species and locality. Tecnomorph, No. G 626. × 30.

There is a low verrucosity on the syllobium and scattered tubercles along the velar edge. The crumina is smooth; the granulosity is hardly noticeable in this species.

Dimensions.—Hinge length–sulcal height of female specimens from Hammarudden: 2085 μ – 1165 μ, 1830 μ – 1020 μ, 1715 μ – 1090 μ.

Remarks.—It is questionable whether this species is closer related to the other *Neobeyrichia* (*Neobeyrichia*) species, from which it differs by its syllobial and velar morphology, than to the two species representing the following subgenus in the sequence of Gotland.

Occurrence.—Hemse Beds: Hammarudden, Medbys, Tjängdarve, Amlings and at the locality near Visne Myr in Fardhem as stated in connection with the neotype selection.

Subgenus *Neobeyrichia* (*Nodibeyrichia*) Henningsmoen 1954

Fig. 140D.

Type Species.—*Beyrichia Bronni* Reuter 1885

Species.—*Neobeyrichia* (*Nodibeyrichia*) *scissa* n.sp.
Neobeyrichia (*Nodibeyrichia*) *regnans* n.sp.
Beyrichia tuberculata Klöden 1834
Beyrichia Bronni Reuter 1885

Diagnosis.—*Neobeyrichia* species with the anterior lobe divided into two lobules and the syllobium often into three, by two subparallel sulcules.

Remarks.—Many of Reuter's (1885, Pl. XXV, etc.) taxia belong to this subgenus. An as yet incomplete investigation of the conditions behind Reuter's lines of lobal development (op. cit., folded plate opposite p. 660) suggests that most of the ostracodes in his *gibbosa–Noetlingi* and *Bronni–Baueri* lines are conspecific; this is possibly true also of *N. tuberculata* and *N. bronni*. The nodes on the three main lobules of the syllobium appear according to a certain pattern, and all transitions are present; it has still to be proved, however, whether this takes place in the same erratic (most of the erratics of *Beyrichia* Limestone are pebble-sized pieces of one limestone bed) or is regional.

Neobeyrichia (*Nodibeyrichia*) *scissa* n.sp.

Fig. 180.

Derivation of the Name.—Latin *scissus* (from *scindere*), cut, referring to the incision in the anterior lobe.

Holotype.—A left female valve, No G 627 (Fig. 180A).

Type Stratum and Type Locality.—Hemse Beds at Hulte, Gotland.

Diagnosis.—*Neobeyrichia* (*Nodibeyrichia*) species with a long anteroventral lobule sharply but more or less incompletely separated from the main part of the anterior lobe, sulcules across the syllobium mostly impossible to trace.

Description.—The lobal cusps protrude over the hingeline; the syllobial cusp is the larger. The sulcule separating the anteroventral lobule mostly does not reach the anteroventral depression. There is a low elevation below the prenodal sulcus connecting the anterior and preadductorial lobes, and the latter lobe and the syllobium are connected by an arched ridge. The velum is markedly set off from the lobal parts of the valve; it forms a wing-like extension behind the crumina, sometimes traced as a bend in the velar outline of the tecnomorphs. There is a low tuberculation on the syllobium and the anteroventral lobule; the velum is finely tuberculate in the adult specimens or shortly spinose anteroventrally; in the tecnomorphs there are often a few widely separated long spines on the velar edge.

Dimensions.—Hinge length–sulcal height of female valves from Hulte: 1705 μ – 1605 μ, 1635 μ – 1065 μ, 1630 μ – 1020 μ.

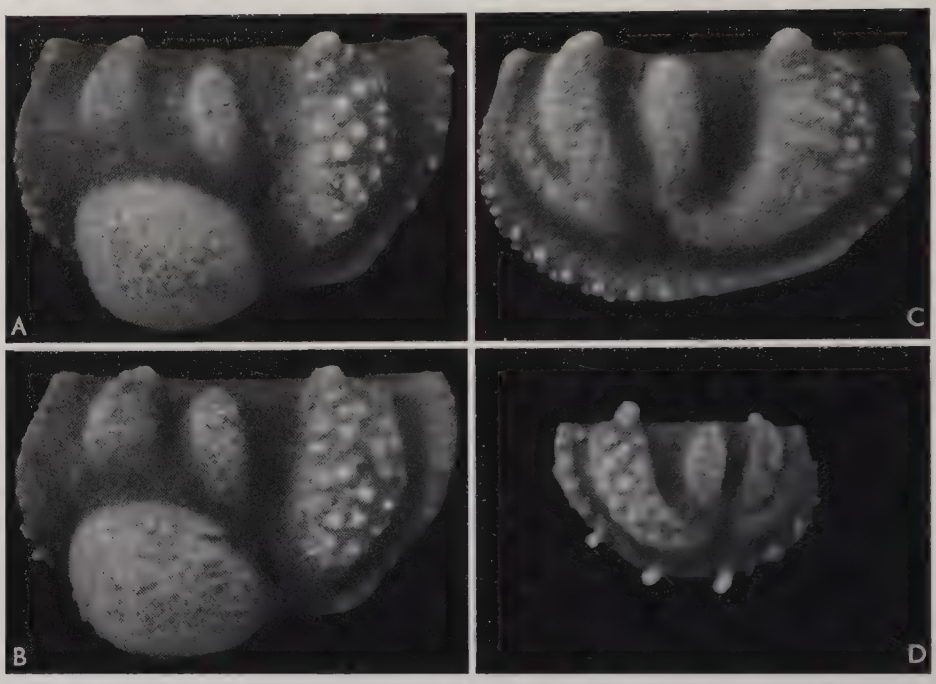


Fig. 180. *Neobeyrichia* (*Nodibeyrichia*) *scissa* n.sp., Hemse Beds, A, B and D from Hulte, C from Gogs. ×30. A. Female, No. G 627 (holotype). B. Female, No. G 629. C. Male, No. G 628. D. Young tecnomorph, No. G 630.

Remarks.—This species differs from the following by the incomplete lobular differentiation both in the anterior lobe and in the syllobium; the species are without doubt closely related.

Occurrence.—Hemse Beds: Gogs, Botvide, Gannor, Fie, Västlaus, Gläves, Hägvide, Hulte, Vanges, Leisungs. Eke Beds: Lingvide, Ronnings.

Neobeyrichia (*Nodibeyrichia*) *regnans* n.sp.

Fig. 181.

Derivation of the Name.—Latin *regnans* (from *regnare*), reigning, referring to the elevated position of the species in the stratigraphy of Gotland.

Holotype.—A left female valve, No. G 631 (Figs. 181 A–B).

Type Stratum and Type Locality.—Hamra Beds at Hoburgen Ia.

Diagnosis.—*Neobeyrichia* (*Nodibeyrichia*) species with a completely isolated, longish anteroventral lobule and shallow sulcular depressions across the syllobium. There is a small striate field on the ventral base of the crumina.

Description.—The lobal cusps are of about the same size and protrude over the hingeline. The only noteworthy lobal connection breaking the sulcal pattern is the arch between the preadductorial knob and the lower part of the syllobium which is, however, comparatively low. The three syllobial lobules as

Fig. 181. *Neobeyrichia* (*Nodibeyrichia*) *regnans* n.sp., Hamra Beds. A and C–E ×30, B ×40. A. Female from Hoburgen I a. No. G 631 (holotype). B. Same specimen (No. G 631, the holotype) in oblique ventral view, anterior end up. C. Male from Hoburgen II b. No. G 632. D. Tecnomorph from Hoburgen. No. G 633. E. Young tecnomorph from Hoburgen. No. G 634.

mentioned in the subgeneric diagnosis are developed; the sulcules separating them vary between ornamented low depressions and deeper furrows without ornamentation. The velum is a well marked ridge with a short, even pointed, wing-like extension behind the crumina; this feature can be traced in the male as an inconsiderable bend in the unornamented ventral part of the velum.

All lobes are markedly verrucose. The velar edge is tuberculate, anteriorly with some small spines. Young tecnomorphs have a few longer spines along the velar edge, usually four or five. The granulosity is somewhat more distinct in this than in other *Neobeyrichia* species.

As seen in Fig. 181 B there is a distinct striate field ventrally on the crumina. There is a low torus at the base of the velar ridge.

Dimensions.—Hinge length–sulcal height of female specimens from Hoburgen Ia: 1995 μ – 1300 μ, 1965 μ – 1145 μ, 1885 μ – 1165 μ.

Remarks.—The development shown by *N. scissa* and *N. regnans* is followed up by *N. tuberculata* in which all lobal units become isolated from each other and the anteroventral lobule becomes large, rounded and almost isolated like the lobes. The three lobules of the broad syllobium are separated by shallower, unornamented sulcules. The lobulation becomes even more complicated by the division of the middle syllobial lobule and by the formation of nodes especially anteriorly on the lower lobule, but also elsewhere. *N. tuberculata* also differs from the Gotland species by having a tuberculo-striate field ventrally on the crumina, not a finger-print striation; the muscle spot in *N. tuberculata* (cf. Bonnema 1913 and Kesling & Wagner 1956) has not been observed in beyrichiines from Gotland. As shown by the valve of *N. protuberans* figured by Bonnema (1913, Fig. 4), obviously a representative of the same genus, species very closely associated with *N. tuberculata* may also exhibit a *Neobeyrichia* (*Neobeyrichia*) stage of lobulation.

Occurrence.—Hamra Beds: Hoburgen Ia, Hoburgen IIa, Hoburgen IIb. Sundre Beds: Juves.

Genus *Calcaribeyrichia* n. g.

Figs. 140 E–F and 182.

Derivation of the Name.—From Latin *calcar*, spur, and the generic name *Beyrichia*, alluding to the development of spur-like spines and lobus associated with them.

Type Species.—*Calcaribeyrichia bicalcarata* n.sp.

Species.—*Calcaribeyrichia bicalcarata* n.sp.
Calcaribeyrichia calcarata n.sp.
Calcaribeyrichia caudata n.sp.
Beyrichia tuberculata var. *Gotlandica* Kiesow 1888
Calcaribeyrichia simplicior n.sp.
Calcaribeyrichia insignior n.sp.

Diagnosis.—*Beyrichiinae* exhibiting a sometimes far-reaching, sometimes inconsiderable dissection of the syllobium and the anterior lobe into lobules, always coupled with a more or less conspicuous development of calcarine, uncular, and acroidal spines. There is in all forms a very small posterior syllobial cusp. Crumina never plicate but sometimes either striate or provided with remains of a velar ridge.

Remarks.—In the lower part of the Hemse Beds in the "eastern facies" forms exhibiting the characters stated in the diagnosis appear in great number; in the Hammarudden–Gannes region almost every small layer investigated has

Fig. 182. *Calcaribeyrichia* n.g. Drawings based on *Calcaribeyrichia bicalcarata* n.sp. ×30. A. Female. B. Male.

its own *Calcaribeyrichia* with a very constant lobal development. However, they have also proved to have a considerable horizontal distribution, and it is difficult to interpret the phenomenon otherwise than as an intense speciation at the beginning of the existence of the genus. Above the Hemse Beds only the characteristically velate *C. bicalcarata* has been found, together with the related but very specialized *Plicibeyrichia*.

C. gotlandica (Kiesow 1888), a tecnomorph with a rounded anteroventral lobule, without spines but with a thickening on the calcarine lobule, has not been identified. The concomitant primitiopsid fauna is easily recognized as coming from the lower part of the Hemse Beds, but the other beyrichiid, represented only by tecnomorphs, in the fauna, *Neobeyrichia* (*Neobeyrichia*) *expansa* Kiesow 1888, also remains unidentified. Probably the fauna comes from the dark shales frequently found along the shores of Östergarn as boulders from submarine exposures.

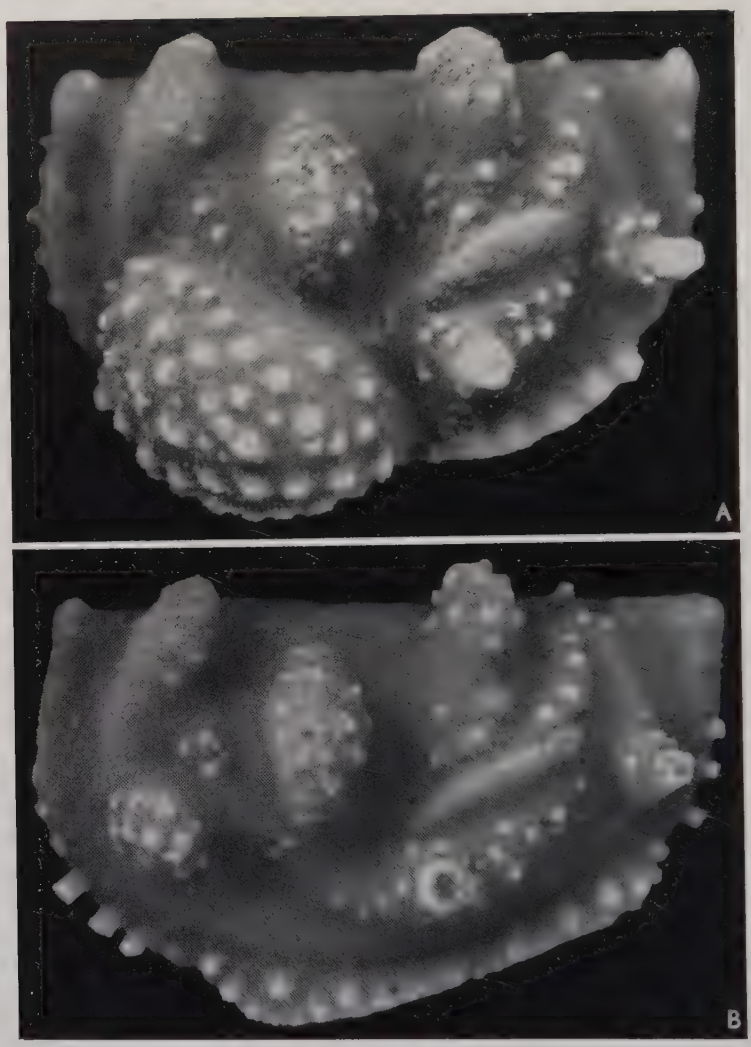


Fig. 183. *Calcaribeyrichia bicalcarata* n.sp., Hamra Beds, Sles. ×40. A. Female valve, No. G 635 (holotype). B. Male valve, No. G 636.

Calcaribeyrichia bicalcarata n.sp.

Figs. 183 and 184.

Derivation of the Name.—Latin *bis*, twice, and *calcaratus*, provided with spurs.

Holotype.—A left female valve, No. G 635 (Figs. 183A and 184).

Type Stratum and Type Locality.—Hamra Beds at Sles, Gotland.

Diagnosis.—*Calcaribeyrichia* with the anterior lobe distinctly split into lobules and with strongly developed calcarine and uncular spines. Velum

Fig. 184. *Calcaribeyrichia bicalcarata* n.sp. The holotype (No. G 635, cf. Fig. 183 A) in ventral view (anterior end up), showing ventral morphology of the velum and the crumina. ×45.

extended ventrally into a characteristic flange with an almost straight edge; in the female a portion of this flange is found on the crumina.

Description.—The cusp of the anterior lobe and the anterior syllobial cusps are high and more or less truncate; the posterior cusp is of the size of a tubercle. In the anterior lobe there is a cuspidal lobule, an anteroventral lobule, and one very small lobule between them and the prenodal sulcus. The preadductorial knob is well isolated. The main lobules in the syllobium are the cuspidal lobule and the calcarine lobule which is long and parallel to the velar edge. Above it there is a deep syllobial groove with a long and thick callus. From the posterior end of the callus to the small posterior syllobial cusp, and down again to the uncular spine there is another, hooked lobular element, the uncular lobule. There is a marked anteroventral depression.

The shape of the velum as mentioned in the diagnosis is seen in Figs. 183 A and 184. There is a constriction separating the portion of the velar flange on the crumina from the postcruminal portion. This part of the velum is tuberculate or verrucose; there are rows of longer spines in front of and behind it. The

crumina is coarsely tuberculate. All shorter lobules are sparsely and more finely tuberculate. In addition to the calcarine and uncular spines mentioned there is also a shorter caudal spine. The granulosity is well developed.

Dimensions.—Hinge length–sulcal height of female specimens from Sles: 2130 μ – 1360 μ, 2030 μ – 1445 μ (compressed).

Remarks.—The present species represents the maximum development along a line of lobular differentiation similar to that in *Neobeyrichia*. In *Calcaribeyrichia*, however, the basic lobular pattern in the syllobium is rather different from the somewhat varying pattern of three subparallel lobules found in *Neobeyrichia*, and it is coupled with a development of lobal spines which is not found in *Neobeyrichia*. Qualitatively, these characters must be regarded as superior to the isolation of the anterior lobe used for the distinction between the two subgenera of *Neobeyrichia*.

For practical reasons the youngest and most advanced *Calcaribeyrichia* species has been described first.

Occurrence.—Eke Beds: Lau Backar. Hamra Beds: Lunde, Sles, Gisle, Norrgårde, and in a sample from the basal Hamra Beds below Hoburgen IIa (not specified on the locality map).

Calcaribeyrichia calcarata n.sp.

Fig. 185.

Derivation of the Name.—Latin *calcaratus*, provided with a spur, referring to the calcarine spine.

Holotype.—A left female valve. No. G 637 (Fig. 185A).

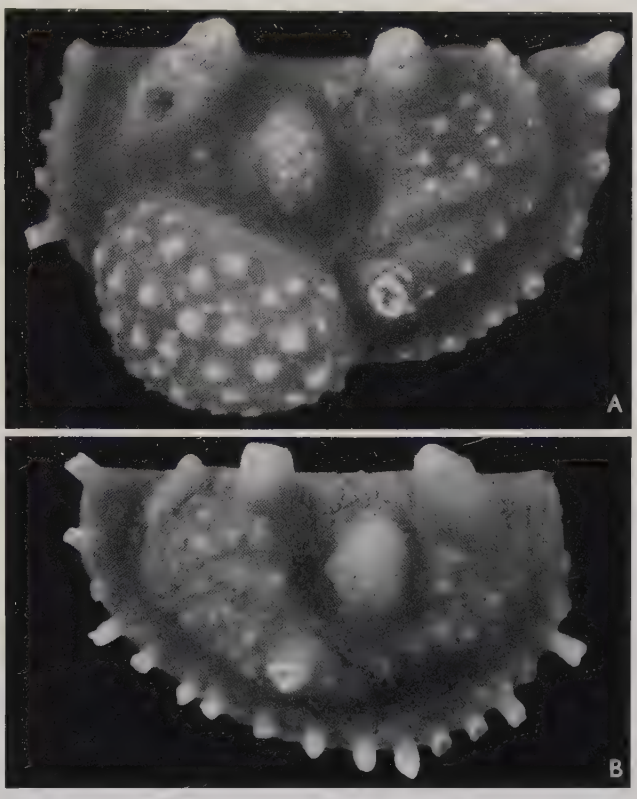
Type Stratum and Type Locality.—Hemse Beds at Hammarudden, Gotland.

Diagnosis.—*Calcaribeyrichia* with indistinct but discernible lobular differentiation and with a strongly developed calcarine spine. No velar specialization in the tecnomorph, except a velar fold ventrally on the crumina, and no differentiation of the tecnomorphic velum.

Description.—The two main lobal cusps are stout and truncate; the posterior syllobial cusp is much smaller than the others but protrudes considerably over the hingeline. The lobular differentiation is best understood starting from the conditions described in *C. bicalcarata*; the three lobular elements of the anterior lobe and lobular elements of the syllobium, including the lobular ridge with the callus, can be traced; the uncular lobule, however, is a simple ridge, only very occasionally ending in a small uncular spine. The calcarine spine, though, is very prominent.

There is a single row of sparsely spaced spines along the well marked velar edge; the caudal spine is of about the same size as the others.

All the lobal parts and the crumina are sparsely verrucose or tuberculate; the crumina has a somewhat coarser and denser ornamentation, without any striation ventrally.



Female valve, bored in the anterior lobe by the organism shown in Fig. 40 A–D. No. G 637 (holotype). ×40.

Tecnomorphic valve, No. G 638. ×40.

Fig. 185. *Calcaribeyrichia calcarata* n.sp., Hemse Beds, Hammarudden.

Dimensions.—Hinge length–sulcal height of female specimens from Hammarudden: 2495 μ – 1510 μ, 2440 μ – 1465 μ, 2365 μ – 1530 μ.

Remarks.—This species exhibits a more primitive lobular development than the preceding, differing further from it by the velar morphology in the tecnomorph. *C. caudata* is relatively closely related to it but represents a trend towards a sharp connecting ridge between the indistinct anteroventral lobule and the calcarine lobule of the tecnomorphs. The lobal spines and the velar edge present further differential characteristics between these species.

Occurrence.—Hemse Beds: Hammarudden, Gannes, Fakle (only tecnomorphs), Sigvalde.

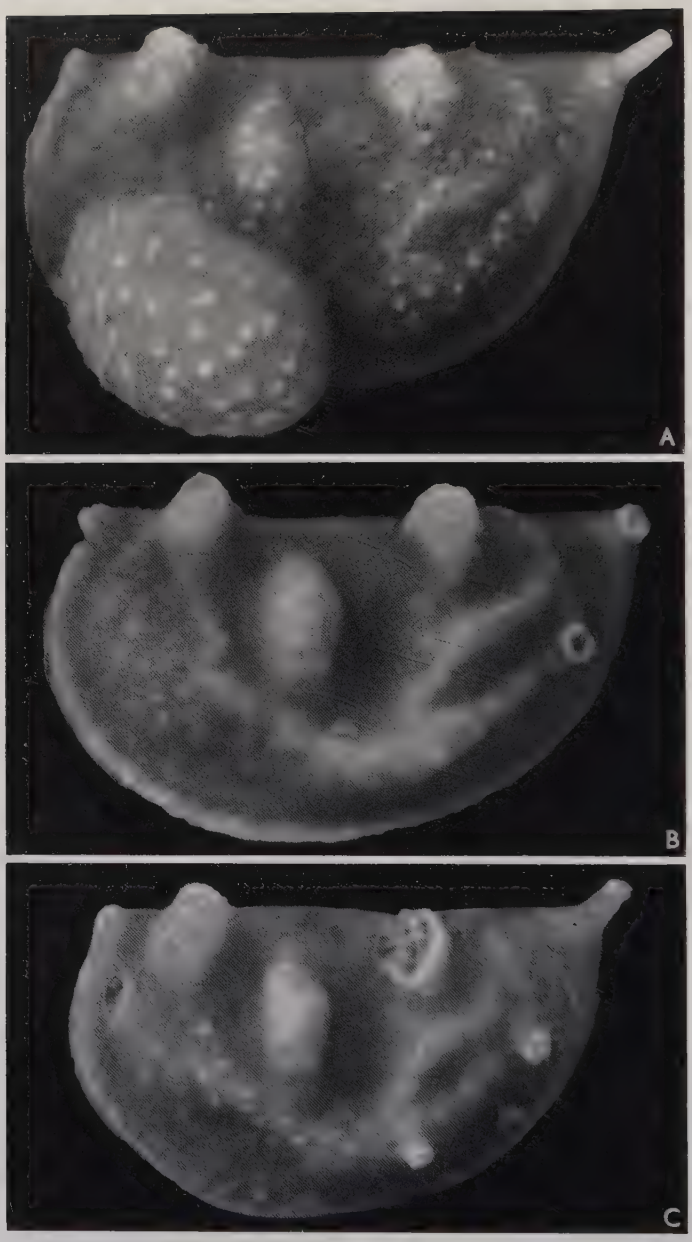
Calcaribeyrichia caudata n.sp.

Fig. 186.

Derivation of the Name.—Latin *caudatus*, provided with a tail, alluding to the extraordinarily long acroidal spine.

Holotype.—A left female valve, No. G 641 (Fig. 186A).

Type Stratum and Type Locality.—Hemse Beds at Tänglings, Gotland.



Female valve. No. G 641. ×40.

Male valve. No. G 642. ×40.

Tecnomorphic valve. No. G 643. ×40.

Fig. 186. *Calcaribeyrichia caudata* n.sp., Hemse Beds, Tänglings.

Diagnosis.—*Calcaribeyrichia* with very diffuse lobular differentiation of the anterior lobe but with a lobal ridge connecting the calcarine and anteroventral lobules, touching the preadductorial knob. Calcarine, uncular, and acroidal spines strongly developed, but occasionally one or even two of them are absent.

Velar ridge undifferentiated, without spines or tubercles; there is a small velar portion ventrally on the crumina.

Description.—The two main lobal cusps are stout and truncate; the posterior syllobial cusp is almost obsolete. The same lobular elements as in the preceding species can be distinguished, but the anterior lobules are very little prominent.The anteroventral lobule is fused with the lateroventral lobal connection which curves over the anteroventral depression and touches the preadductorial knob; sometimes the ridge even bifurcates by fusion with the two anterior lobules. The calcarine lobule and the callic lobule are about of equal shape but not always very sharp; the callus is so near to the uncular lobule that the hook is contracted to a ridge. The lobal ornamentation is a low verrucosity; a more distinct verrucosity is found on the crumina.

Dimensions.—Hinge length–sulcal height of female specimens from Tänglings: 1905 μ – 1150 μ, 1865 μ – 1100 μ, 1765 μ – 1090 μ.

Remarks.—This species shows affinities with especially *C. calcarata*; they are discussed under that species.

Occurrence.—Hemse Beds: Tänglings.

Calcaribeyrichia simplicior n.sp.

Figs. 187 and 188.

Derivation of the Name.—Comparative of Latin *simplex*, simple.

Holotype.—A right female valve, No. G 644 (Fig. 187A).

Type Stratum and Type Locality.—Hemse Beds at Hammarudden, Gotland.

Diagnosis.—*Calcaribeyrichia* almost lacking lobular differentiation but with a mostly very prominent calcarine spine, often with a caudal spine and with a spine very near the edge of the velum at the end of the very indistinct uncular lobule. There is no velar edge on the crumina.

Description.—The two main lobal cusps are stout and truncate; the posterior syllobial cusp is of tubercle size or is obsolete. There are traces—or rather oriments—of an uncular ridge and a syllobial callus and mostly unornamented depressions below the main cusps as the only signs of the more advanced lobulation in other *Calcaribeyrichia* species. There is almost no anteroventral depression. All lobes are tuberculate. The crumina is tuberculate or verrucose all around (Fig. 188B); there is no velar edge on the crumina, but at the cruminal base near the edge the granules in the granulation tend to fuse and form a few lines in a striate pattern like that in more primitive *Beyrichiinae*.

Dimensions.—Hinge length–sulcal height of female specimens from Hammarudden: 2145 μ – 1385 μ, 2015 μ – 1285 μ, 1375 μ – 1240 μ.

Remarks.—This species is the most primitive *Calcaribeyrichia* both with respect to cruminal morphology and to lobulation and does not differ much in the general lobal pattern from those *Beyrichia* (*Simplicibeyrichia*) species which

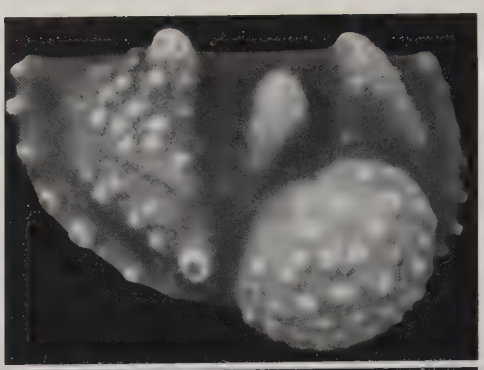


Fig. 187 A. *Calcaribeyrichia simplicior* n.sp., Hemse Beds, Hammarudden. Female, No. G 644 (holotype). × 30.

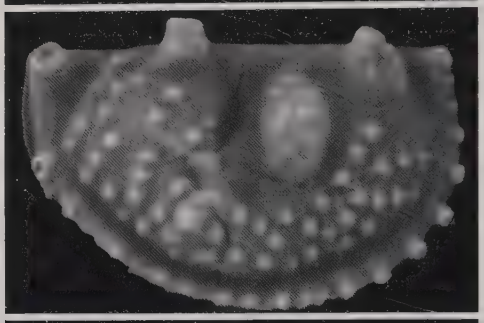


Fig. 187 B. Same species and locality. Male, No. G 645. × 30.

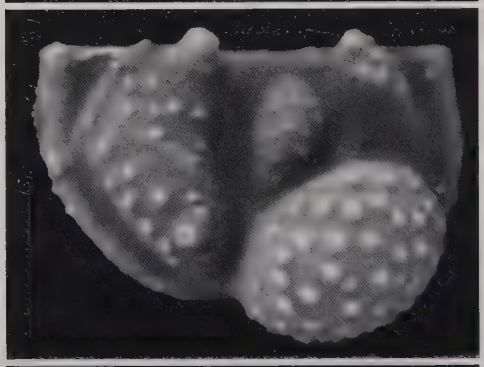


Fig. 187 C. Same species, Hemse Beds, Skåne. Female, No. G 646. × 30.

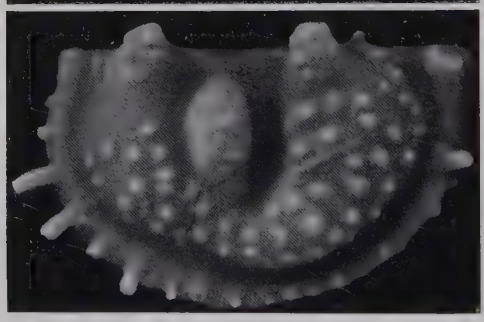


Fig. 187 D. Same species, Hemse Beds, Skåne. Male, No. G 647. × 30.

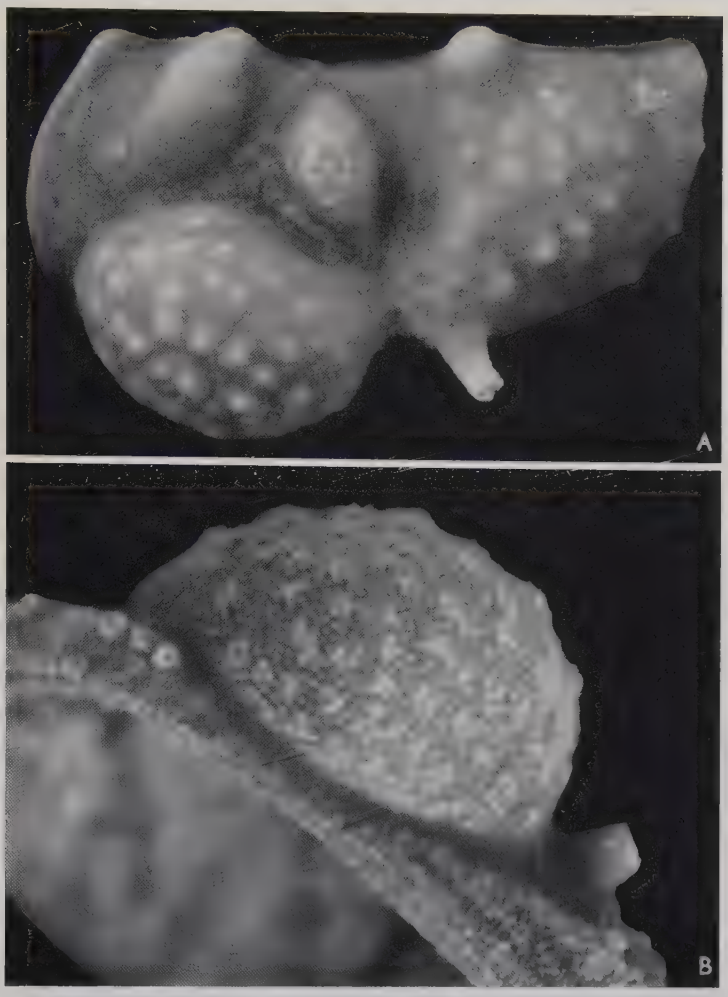


Fig. 188. *Calcaribeyrichia simplicior* n.sp., Hemse Beds, Hammarudden. A. Female valve, slightly folded, with prominent calcarine spine. No. G 639. ×40. B. Crumina from the ventral side (anterior end towards the upper left corner). No. G 640. ×60.

appear at the same time. The ventral morphology of the crumina, however, clearly shows the obsoletion of the finger-print striation at the same time as the absence of a velar ridge distinguishes it from the *Calcaribeyrichia* species described above.

Occurrence.—Hemse Beds: Hammarudden, Grogarns, Skåne, Sigvalde, Tänglings.

Calcaribeyrichia insignior n.sp.

Fig. 189.

Derivation of the Name.—Comparative of Latin *insignis*, (finely) adorned.

Holotype.—A left female valve, No. G 648 (Fig. 189A).

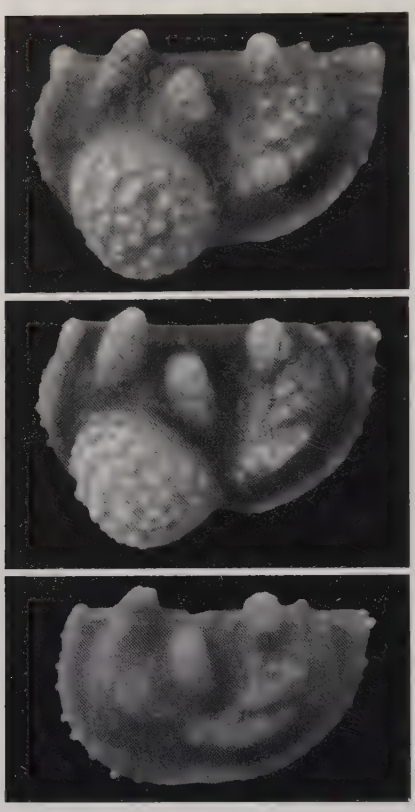


Fig. 189 A. *Calcaribeyrichia insignior* n.sp., Hemse Beds, Hammarudden. Female, No. G 648 (holotype). × 30.

Fig. 189 B. Same species and locality. Female, No. G 649. × 30.

Fig. 189 C. Same species and locality. Tecnomorph, No. G 650. × 30.

Type Stratum and Type Locality.—Hemse Beds at Hammarudden, Gotland.

Diagnosis.—Small *Calcaribeyrichia* species with complete lobular development but without spines. There is an often striate portion of the velar ridge on the crumina.

Description.—The two main lobal cusps are stout and rounded, and there is mostly a small posterior syllobial cusp on the upper end of the uncular lobule. The middle lobule of the anterior lobe tends to become larger than in the other species; the calcarine lobule has a callic thickening like the lobule above it. The anteroventral depression is relatively more marked than in the other species. The lobes are verrucose.

The velum is very slightly extended along the ventral part of the valve; this portion is not tuberculate like the anterior and posterior parts of the velar ridge. The crumina is tuberculate with a portion of the velar ridge set off as in the three other lobulate species described, However, the inner side of the ridge is striate which might indicate that the velar ridge found in some *Calcaribeyrichia* species is a secondary plication immediately laterally to the homo-

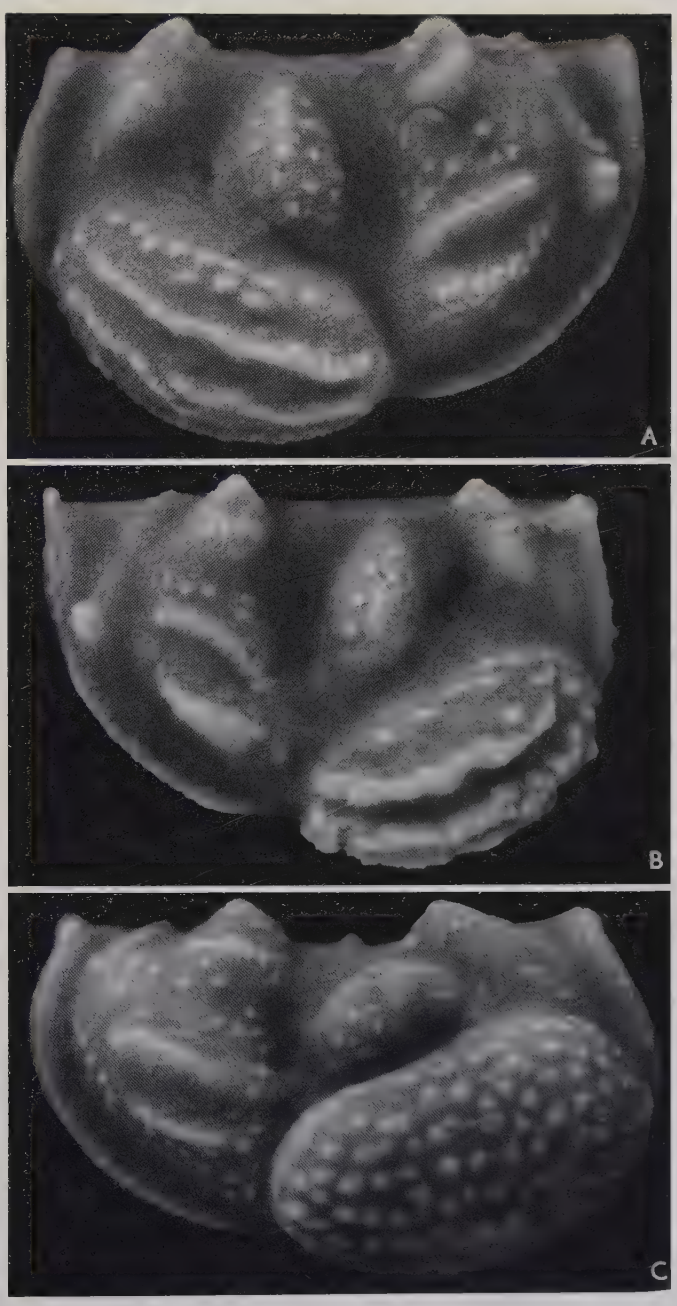


Fig. 190. A–B. *Plicibeyrichia ornatissima* n.sp. ×40. A. Eke Beds, Lau Backar, female valve, No. G 651. B. Hamra Beds, Sles, female valve, No. G 652 (holotype). C. *Plicibeyrichia* aff. *ornatissima*, Hemse Beds, Botvide, No. G 653. ×40.

logue of a real velar edge. It would, then, be homologous to the bulge immediately distally of the striation in *C. simplicior*.

Dimensions.—Hinge length–sulcal height of specimens from Hammarudden, in microns: 1465–860, 1445–830, 1430–890, 1405–810, 1385–845.

Remarks.—Already the description comprises a comparison with the other *Calcaribeyrichia* species; two exclusive differential diagnostics are the small size and the absence of spines.

Occurrence.—Hemse Beds: Hammarudden, Tänglings.

Genus *Plicibeyrichia* n.g.

Derivation of the Name.—Latin *plica*, fold, and the generic name *Beyrichia*.

Type Species.—*Plicibeyrichia ornatissima* n.sp.

Species.—Only the type species.

Diagnosis.—*Beyrichiinae* with fold-like lobules of which the units on each side of the syllobial groove are especially prominent; plications also occur on the crumina. The sharply ridge-like uncular lobe tends to become united with the anteroventral lobule.

Remarks.—The development of fold-like lobules with crests very similar to a callus, one of which tends to become united with the anteroventral lobule into a lateroventral lobe, continues through the genus *Gannibeyrichia* and reaches its maximum in *Navibeyrichia*.

Plicibeyrichia ornatissima n.sp.

Figs. 190A–B and 191.

Derivation of the Name.—Superlative of Latin *ornatus*, ornate.

Holotype.—A left female valve, No. G 652 (Fig. 190B).

Type Stratum and Type Locality.—Hamra Beds at Sles, Gotland.

Diagnosis.—As for the genus.

Description.—In the tecnomorph the preadductorial node is isolated. The lateroventral lobe has a callic swelling along the calcarine part of its crest; in smaller moult stages it proves to have originated around a calcarine tubercle which becomes obsolete in adult specimens. The callus is very conspicuous, and there are callus-like or cristal fusions of the granulation even on the preadductorial node and the two major lobal cusps but not on the uncular lobule which has a small uncular spine even in adult specimens. The posterior syllobial cusp is very small. Along the velar edge there is an ornamental ridge like that in the *Craspedobolbininae*.

The adult female has one short callus on each side of the syllobial groove. The crumina is longitudinally plicate with callus-like ridges formed by the fusion of granules and tubercles. Ventrally there is a portion of the velar edge on the crumina as in *Calcaribeyrichia;* there is a toric ridge, distinct only along the edge of the postcruminal portion of the velum.

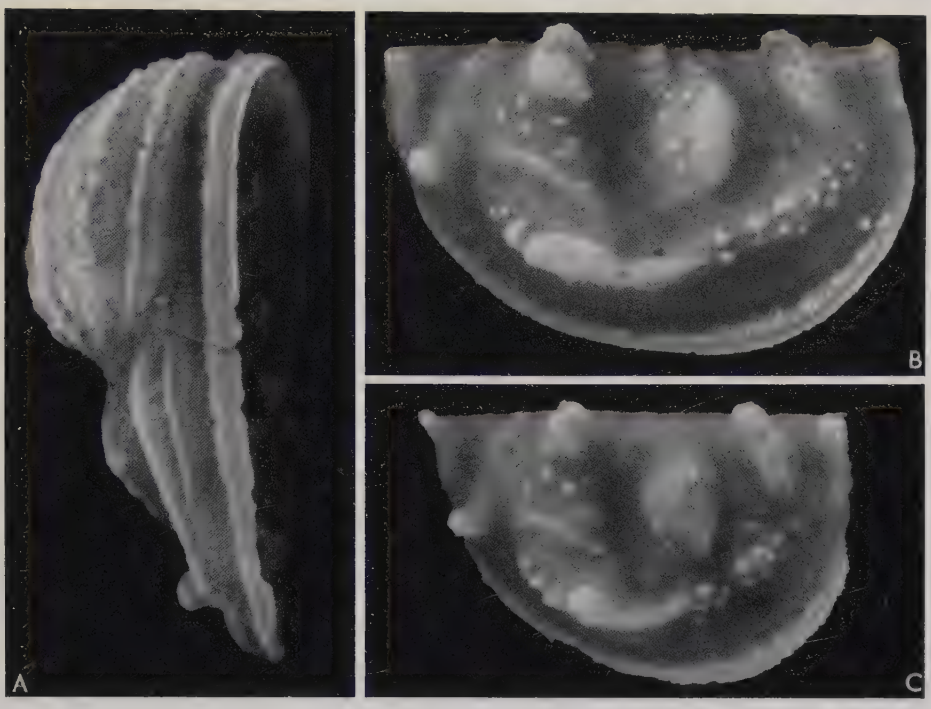


Fig. 191. *Plicibeyrichia ornatissima* n.sp. × 40. A. Female valve in ventral view (anterior end up), from the Eke Beds at Lau Backar. No. G 654. B. Tecnomorph from the Hamra Beds at Sles. No. G 655. C. Younger tecnomorph from the same locality. No. G 656.

Dimensions.—Hinge length–sulcal height of female specimens from Sles: 2065 μ – 1230 μ, 1865 μ – 1090 μ.

Remarks.—A specimen with an evenly tuberculate crumina, lacking plications, without an uncular spine but with a small cusp above the adductorial sulcus, has been found in the Hemse Beds at Botvide. It has a velar ridge ventrally on the crumina. It is figured here as *P.* aff. *ornatissima* (Fig. 190C).

Occurrence.—Eke Beds: Lau Backar. Hamra Beds: Lunde, Sles. Sundre Beds: Juves.

Genus *Gannibeyrichia* n.g.

Fig. 140G.

Derivation of the Name.—From the stem in *Gannes* and the generic name *Beyrichia.*

Type Species.—*Gannibeyrichia gannensis* n.sp.

Species.—*Gannibeyrichia biplicata* n.sp.

Gannibeyrichia gannensis n.sp.

Diagnosis.—*Beyrichiinae* with a lateroventral lobe and a restriction of the velar edge behind the crumina.

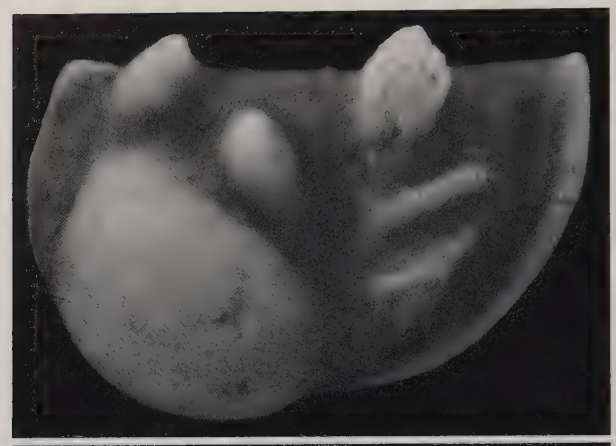


Fig. 192 A. *Gannibeyrichia biplicata* n.sp., Eke Beds, Lau Backar. Female, No. G 657 (holotype). × 40.

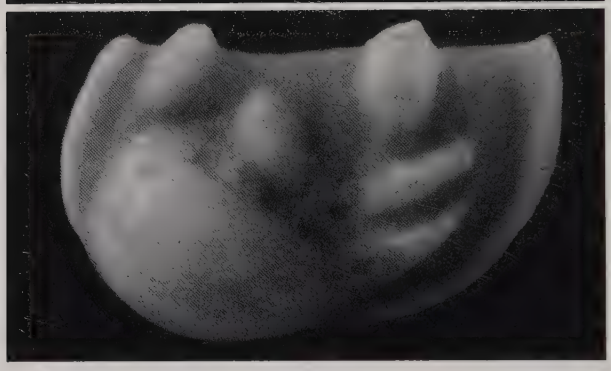


Fig. 192 B. Same species and locality. Female, No. G 658. × 40.

Gannibeyrichia biplicata n.sp.

Figs. 192 and 193.

Derivation of the Name.—Latin *bis*, twice, and *plicatus*, folded, alluding to the syllobial morphology.

Holotype.—A left female valve, No. G 657 (Fig. 192A).

Type Stratum and Type Locality.—Eke Beds at Lau Backar, Gotland.

Diagnosis.—*Gannibeyrichia* species with free lateroventral lobe.

Description.—Anterior lobe with protruding cusp. Preadductorial knob isolated. In the tecnomorph there is a lateroventral lobe with a secondary crista from the lower part of the anterior lobe to the end of the calcarine lobule. Above this lobule there is a callic lobule with a similar secondary crista. The stout syllobial cusp is isolated from the other lobules by a deep sulcule. The crumina is very large and separated from the cusp of the anterior lobule by a narrow sulcule.

The crumina has a velar ridge and a torus along it; the torus is interrupted behind the crumina but otherwise developed in the same way both on the crumina and the post-cruminal velar portion. The velum has an ornamental thickening along the edge.

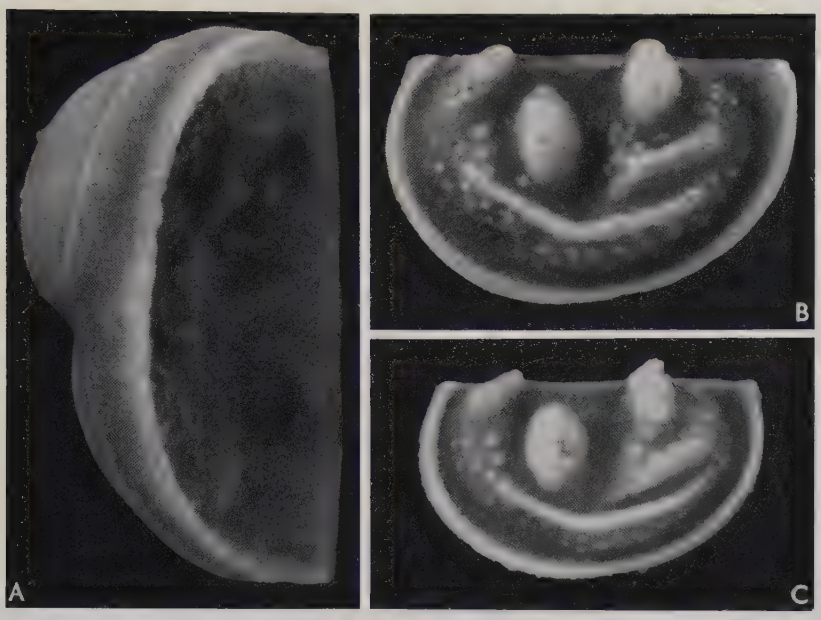


Fig. 193. *Gannibeyrichia biplicata* n.sp., Eke Beds, Lau Backar. × 40. A. Female valve in ventral view (anterior end up), No. G 659. B. Tecnomorph, No. G 660. C. Younger tecnomorph, No. G 661.

The tecnomorphs have a fine verrucosity on the lobes; the females are smooth. There are no spines in any part of the animal.

Dimensions.—Hinge length–sulcal height of female specimens from Lau Backar: 1730 μ – 1120 μ, 1630 μ – 985 μ, 1610 μ – 985 μ.

Remarks.—This species differs from the following especially by the extension of the crumina along the anterior lobe, the well isolated lateroventral lobe, the distinctly biplicate arrangement of the syllobium in the female, and by the velar edge on the crumina which is only a little curved and is accompanied by a torus.

Occurrence.—Eke Beds: Lau Backar (rare).

Gannibeyrichia gannensis n.sp.

Fig. 194.

Derivation of the Name.—From the stem in the locality name of Gannes, referring to the occurrence of this species at Gannes and in the cliffs of Gannberget.

Holotype.—A right female valve, No. G 663 (Fig. 194B).

Type Stratum and Type Locality.—Hemse Beds at Gannes, Gotland.

Diagnosis.—*Gannibeyrichia* species in which the lateroventral lobe touches the preadductorial knob and both ends of the callic lobule.

Fig. 194. *Gannibeyrichia gannensis* n.sp. A. Female, No. G 662. × 30. B. Female, No. G 663 (holotype). C. Male, No. G 664. × 30. D. Tecnomorph, No. G 665. E. Female carapace in ventral view (anterior end up), No. G 666. F. Female carapace with same orientation, No. G 667. Hemse Beds, Gannes. A–D × 30, E–F × 40.

DESCRIPTION.—The two lobal cusps are stout and very protruding. The cuspidal part of the anterior lobe is separated from the lateroventral lobe by a shallow, wide sulcular depression. The area between the lobules of the syllobium and the posterior margin is remarkably wide. In the female the syllobial lobules are more or less fused. The tecnomorphic velum is wide. The postcruminal portion of the velum is narrower, well developed with a marked edge and torus only on a short, somewhat protruding portion just behind the constriction. On the crumina there is a curved ridge which seems to be the velar edge; the torus in this species can be very prominent, and it can be questioned whether the ridge is not toric in origin. The crumina is rounded next to the cuspidal part of the anterior lobe and separated from it by a wide sulcular depression. The state of preservation does not allow a closer study of the ornamentation.

DIMENSIONS.—Hinge length–sulcal height of female specimens from Gannes: 2065 μ – 1320 μ, 2030 μ – 1270 μ, 2015 μ – 1300 μ.

REMARKS.—The main differential characters are summed up under the preceding species.

OCCURRENCE.—Hemse Beds: Gannes, Fakle.

Genus *Navibeyrichia* n.g.

Figs. 140H and 195.

DERIVATION OF THE NAME.—Latin *navis*, ship, and the generic name *Beyrichia*.

TYPE SPECIES.—*Navibeyrichia hanseatica* n.sp.

SPECIES.—*Navibeyrichia hanseatica* n.sp.
Navibeyrichia balticivaga n.sp.
Beyrichia Damesii KRAUSE 1891

DIAGNOSIS.—*Beyrichiinae* with a lateroventral lobe. The crumina is almost incorporated with the carapace, and the velar edge and the torus pass across it without interruption.

REMARKS.—It is fairly difficult to estimate the relationships of this genus. The morphology of the lateroventral lobe suggests an extreme development along lines similar to those illustrated by the preceding genera. But there are also features in the lobation similar to the conditions in *Beyrichia* (*Asperibeyrichia*), such as the development of a small lobule above the crumina and a faint zygal connection. Most probably, however, the homoeomorphic tendencies in the lobal development are connected with the far-reaching invasion of carapace wall elements by the crumina; the velar development and the fold-like lobation are decisive for the placing of *Navibeyrichia* in the system.

Navibeyrichia hanseatica n.sp.

Figs. 196A–B.

DERIVATION OF THE NAME.—Latin *Hanseaticus*, referring to some similarity of the species to the hull of a Hanseatic merchant ship.

Fig. 195. *Navibeyrichia* n.g. Drawing based on *Navibeyrichia hanseatica* n.sp. ×40. A. Female. B. Male.

Holotype.—A right female valve, No. G 668 (Fig. 196A).

Type Stratum and Type Locality.—Hemse Beds at Tänglings, Gotland.

Diagnosis.—*Navibeyrichia* species with only a very low, verrucose lobule between the crumina and the prenodal sulcus.

Description.—Lobal features, even the secondarily cristate lateroventral lobe, fairly rounded. The lobal cusps are rounded but concealed by tubercles or short spines; the posterior syllobial cusp is sometimes free and pointed but always very small. There is a low zygal connection between the preadductorial knob and the syllobium in the tecnomorphs. The most protruding parts of the lobes have wide smooth areas; this is true for the lobal cusps, the preadductorial knob, and the cristal part of the lateroventral lobe. On the crumina there is a similar area. There is a sparse verrucosity both on the lobes and the velar ridge. The anteroventral part of the crumina is verrucose, and a similar ornamentation is found also on the small lobule above the crumina.

Dimensions.—Hinge length–sulcal height of female specimens from Tänglings: 1530 μ – 1000 μ, 1500 μ – 965 μ, 1370 μ – 870 μ.

Remarks.—This species differs from both the other *Navibeyrichia* species by not having a well developed lobule along the crumina and by its spinose and dissected lobal cusps.

Occurrence.—Hemse Beds: Hammarudden, Hammars, Tänglings, Sigvalde.

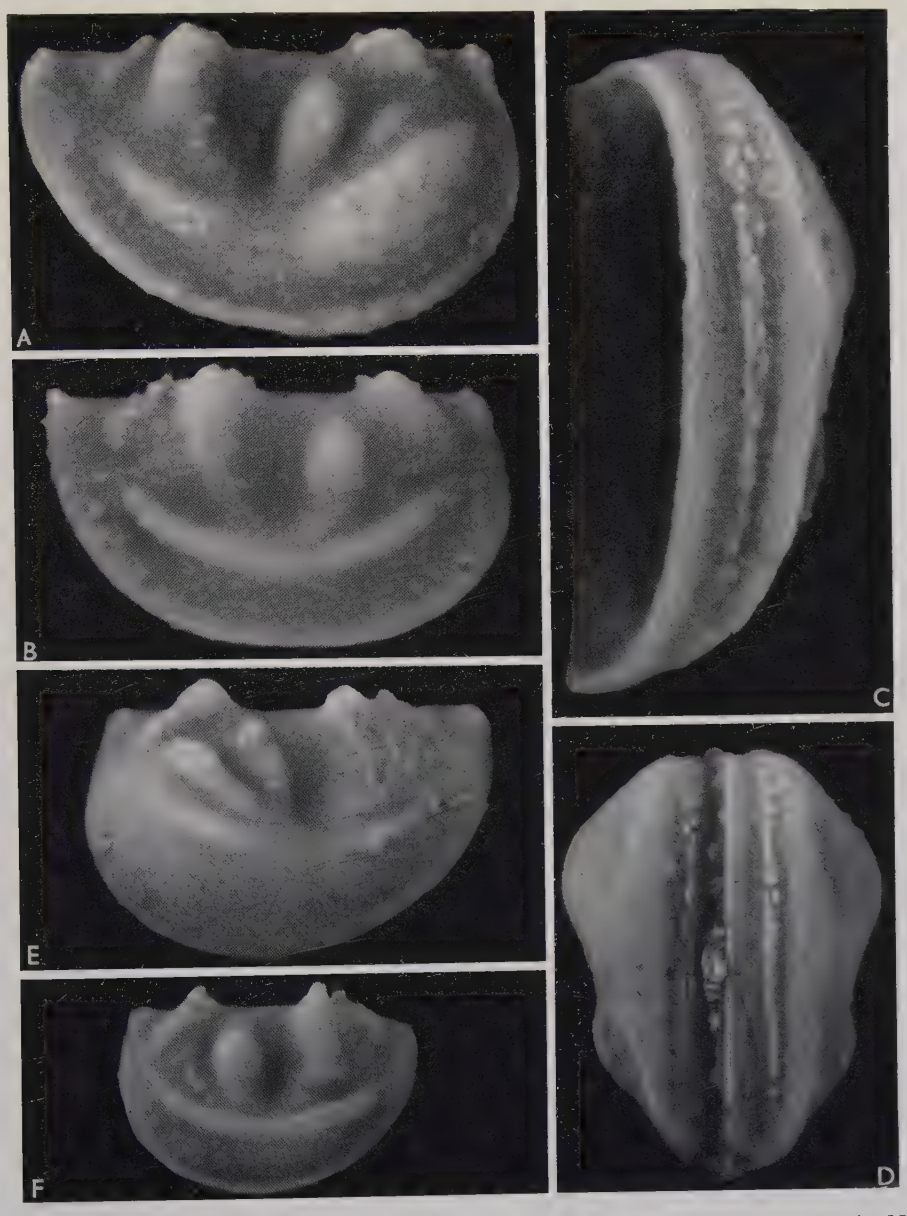


Fig. 196. A–B. *Navibeyrichia hanseatica* n.sp., Hemse Beds, Tänglings. ×40. A. Female, No. G 668 (holotype). B. Male, No. G 669. C–F. *Navibeyrichia balticivaga* n.sp., Hamra Beds, Norrgårde. C. Left female valve in ventral view (anterior end up) RM No. Ar 26062:1. ×60. D. Female carapace with the same orientation, RM No. Ar 26062:3. ×40. E. Female, RM No. Ar 26062:11 (holotype). ×40. F. Tecnomorph, RM No. Ar 26062:13. ×50.

Navibeyrichia balticivaga n.sp.

Figs. 196C–F.

Derivation of the Name.—Latin (*mare*) *Balticum*, the Baltic, and *-vagus*, rambling.

Holotype.—A left female valve, RM No. Ar 26062:11 (Fig. 196E).

Type Stratum and Type Locality.—Hamra Beds at Norrgårde, Gotland.

Diagnosis.—*Navibeyrichia* species with a marked lobule between the crumina and the prenodal sulcus but no similar lobule in the male.

Description.—Lobal features sharp. All cusps pointed, without accessory spines. The posterior syllobial cusp is considerably smaller than the others. The smooth areas on the lobes are narrower and better defined than in the preceding species. Particularly the lateroventral lobe is very sharp, of cristate appearance. The low zygal arch is partly assimilated by the lateroventral lobe. The crumina is more tumid and occupies more of the carapace space than that of the preceding species; there is only a very small part of the lateroventral lobe to be seen behind the crumina. Below the characteristic lobule along the crumina there is one more ridge, corresponding to the wider smooth area in *N. hanseatica*. Tecnomorph sparsely verrucose; the female is verrucose only on the syllobium. There is, then, no verrucose field along the velar edge on the crumina and no verrucosity on the lobule above it.

Dimensions.—Hinge length–sulcal height of female specimens from Norrgårde: 1360 μ – 845 μ, 1300 μ – 830 μ, 1085 μ – 730 μ.

Remarks.—This species is similar to *N. damesi* but differs from it in lacking a lobule above the anterior part of the lateroventral lobule in the tecnomorph. Even if only one tecnomorphic specimen of each species is known, this feature cannot be expected to vary in this way within a species. Krause's original material has been examined. It is not very similar to the figures (cf. Krause 1891, Pl. XXXII, figs. 1–3).

Occurrence.—Hamra Beds: Norrgårde.

Genus *Bingeria*

Figs. 140A and 197.

Derivation of the Name.—Latin *Bingerius*, from Bingers.

Type Species.—*Bingeria zygophora* n.sp.

Species.—*Bingeria zygophora* n.sp.

Craspedobolbina expansinodata (Henningsmoen 1954)

Bingeria cyamoides n.sp.

Diagnosis.—Irregularly reticulate *Beyrichiidae* with an anteroventral, ventrally striate crumina and a fused beyrichiine lobation with long, curved cuspidal ridges. The cuspidal plica of the anterior lobe continues over the preadductorial node but disappears without forming a node at the end.

Remarks.—This is the only European genus of a group of genera, represented

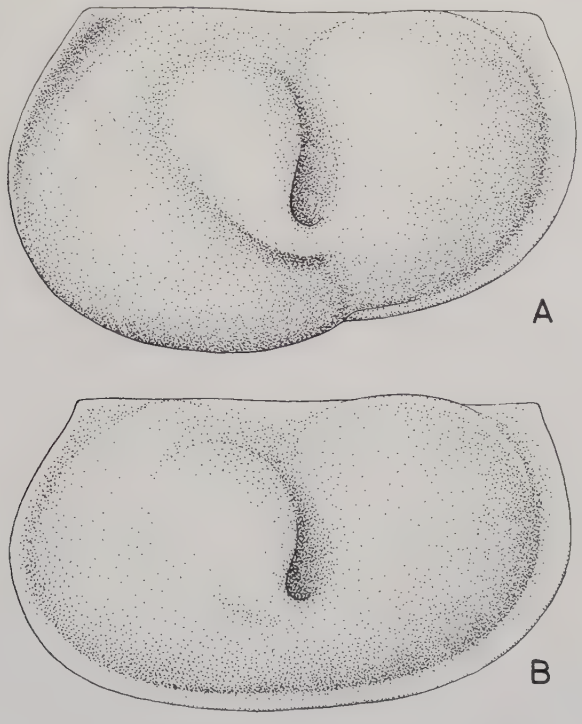


Fig. 197. *Bingeria* n.g. Generalized drawing (the complicated reticulation omitted) based on *Bingeria zygophora* n.sp. ×30. A. Female. B. Male.

in North America by several species belonging to the genera *Lophokloedenia*, *Welleriopsis*, *Zygobeyrichia*, and *Kloedenia sensu* SWARTZ & WHITMORE 1956 (as briefly discussed below *Kloedenia* is quite another type of ostracode than those traditionally referred to this genus in North America). It is very doubtful whether these genera belong to the *Beyrichiinae* at all, but a more extensive analysis of the velar and cruminal morphology has to be made also on the abundant and varied American material before they can be separated from this subfamily. At any rate they constitute a very independent branch of beyrichiine development with an ornamentation radically differing from all other *Beyrichiinae*. Also the morphology of the flange-like velum is very different from that in other *Beyrichiinae*.

Bingeria zygophora n.sp.

Figs. 198 and 199.

DERIVATION OF THE NAME.—Latinized Greek *zygophorus*, yoke-bearing, referring to the rudimentary zygal ridge in the species.

HOLOTYPE.—A left female valve, No. G 672 (Fig. 198C).

TYPE STRATUM AND TYPE LOCALITY.—Tofta Beds at Annelund, Gotland.

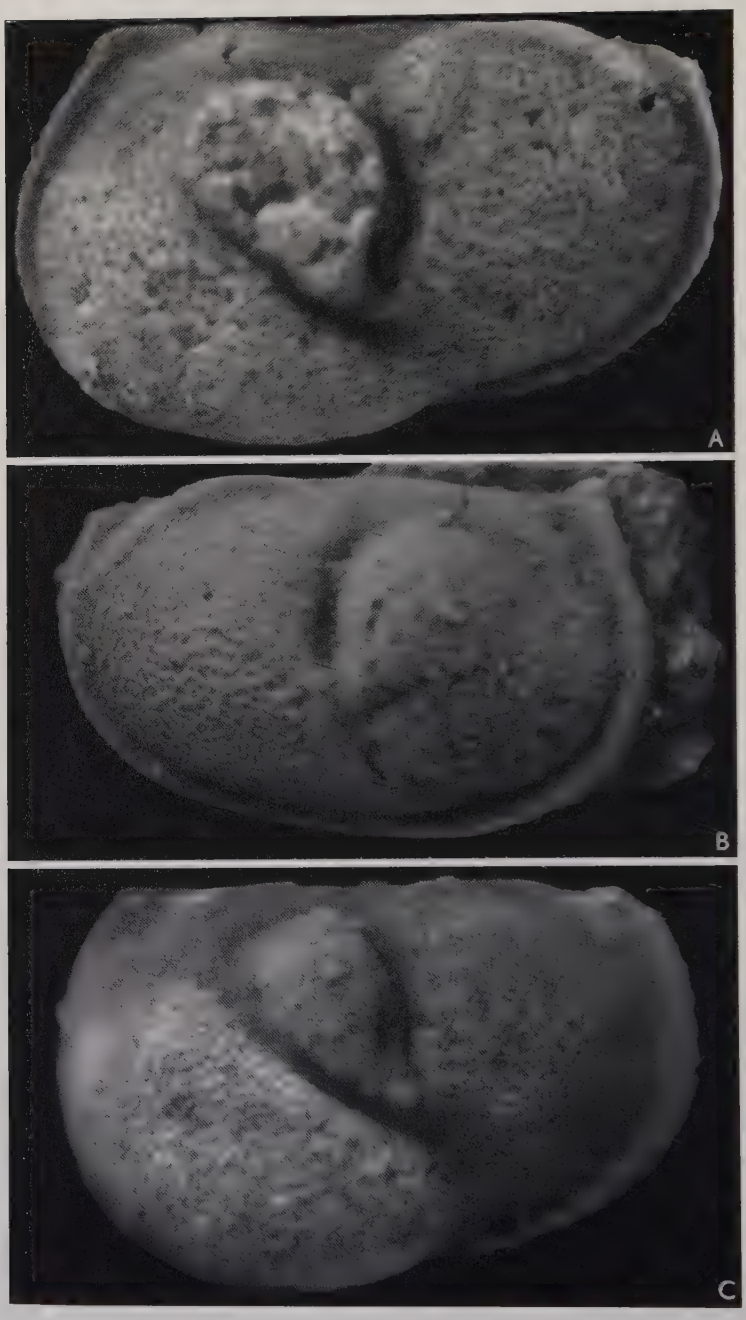


Fig. 198. *Bingeria zygophora* n.sp. Tofta Beds. × 40. A. Female valve from Bingers, No. G 670. B. Tecnomorph from Annelund, No. G 671. C. Female valve from Annelund, No. G 672 (holotype).

Fig. 199. *Bingeria zygophora* n.sp. The holotype (No. G 672) in oblique ventral view (anterior end up). ×40.

DIAGNOSIS.—*Bingeria* species with a zygal connection below the adductorial sulcus and distinct cuspidal ridges. Tumid crumina with a very deep furrow limiting it from the preadductorial node.

DESCRIPTION.—The anterior lobe in the tecnomorph is gently rounded and fused with the preadductorial node so that only the lowermost part of the prenodal sulcus is visible as a narrow furrow. The cuspidal ridge of this lobe disappears near the hinge margin above the preadductorial node. The preadductorial node is very large; only in the female is it well delimited anteriorly, and the zygal connection becomes distinct. Also the syllobium is gently rounded, without a groove but with a sharp, ridgelike cuspidal plica. The crumina reaches very slightly behind the very narrow adductorial sulcus. The velar flange is comparatively narrow and thin. An irregular reticulation (Fig. 198) covers all lobal parts and the crumina; there is a striate bulge ventrally on the crumina (Fig. 199).

DIMENSIONS.—Hinge length–sulcal height of a female specimen from Bingers 1995 μ – 1330 μ, of a female specimen from Annelund 1815 μ – 1295 μ.

REMARKS.—The present species is considerably larger than *B. expansinodata* (total length of females 1750–900 μ) and differs further from it by the deep furrow behind the crumina. This is, otherwise, one of the very few close relationships proved between Silurian ostracodes from Gotland and Norway (cf. the following species). *Craspedobolbina dorsoplicata* HENNINGSMOEN 1954

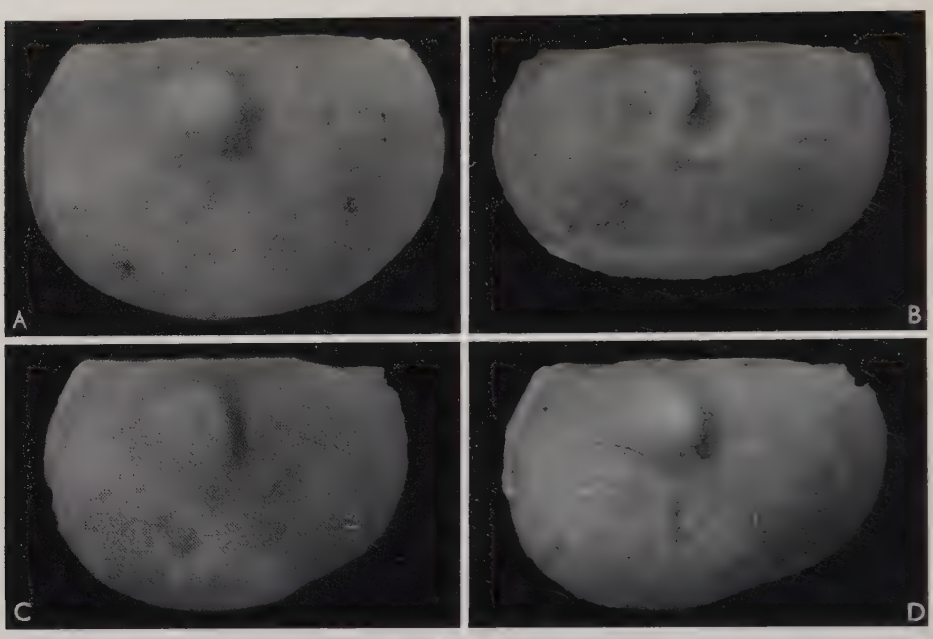


Fig. 200. *Bingeria cyamoides* n.sp., Tofta Beds, A–B from Bingers, C–D from Annelund. · 30. A. Female, No. G 674. B. Tecnomorph, No. G 676. C. Female, No. G 675. D. Female, No. G 677 (holotype).

(op. cit., Pl. 4, figs. 6–8; not Pl. 5 figs. 1–3) also shows the lobal characteristics of *Bingeria*, but the characteristic reticulation cannot be observed in the figures; the original material has not been examined.

Occurrence.—Tofta Beds: Annelund, Galgberget, Bingers.

Bingeria cyamoides n.sp.

Fig. 200.

Derivation of the Name.—Latinized Greek *cyamoides*, bean-like.

Holotype.—A left female valve, No. G 677 (Fig. 200 D).

Type Stratum and Type Locality.—Tofta Beds at Annelund, Gotland.

Diagnosis.—*Bingeria* species with a very low velar ridge, a pit-like sulcus behind the preadductorial node which is completely fused with the anterior lobe, faint cuspidal ridges and a long crumina, also comprising the anteroventral part of the syllobium, not markedly set off from the lobal parts of the valve.

Description.—The diagnosis has only to be completed with the statements that the outline is subamplete, that traces of a zygal connection can be observed in the tecnomorphs, and that all lobal parts of the valve and the crumina are covered by a fine reticulation.

Dimensions.—Hinge length–sulcal height of female valves from Annelund: 1595 μ – 1100 μ, 1530 μ – 1165 μ, 1530 μ – 1145 μ.

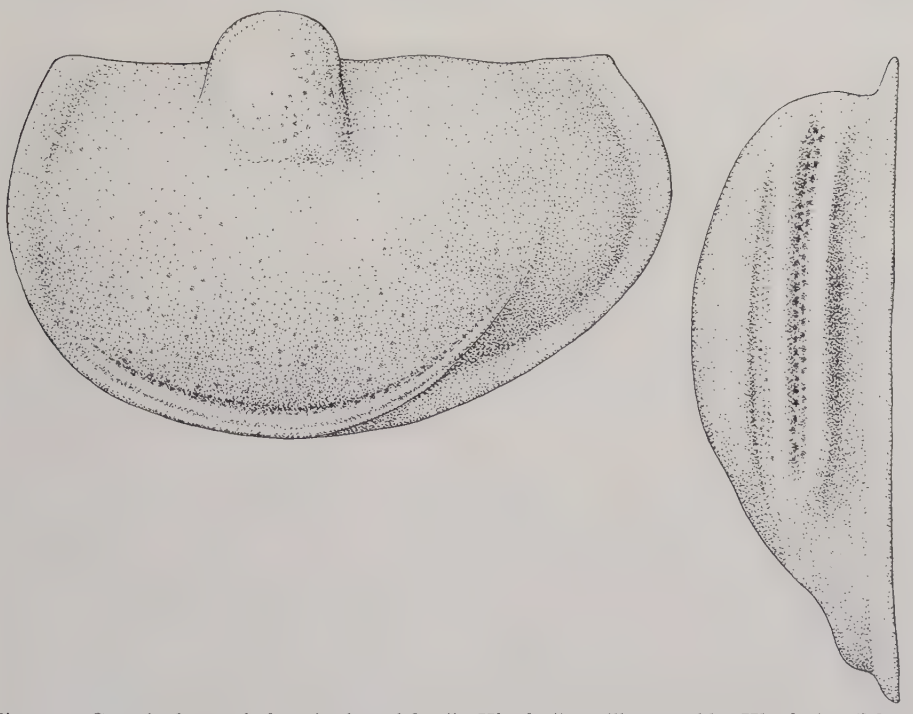


Fig. 201. Cruminal morphology in the subfamily *Kloedeniinae*, illustrated by *Kloedenia wilckensiana* (Jones 1855), generotype of *Kloedenia*. Drawing based on photographs published by Kesling (1956 b, especially No. 32759, Pl. VI, figs. 6–8). ×35.

[The drawing is based on weathered originals. As later shown by unweathered material the inner and middle cruminal crests are pronouncedly striate, and a fine striation is also to be found on the outer crest.]

Remarks.—There is a very similar species in the Silurian of Norway, described by Henningsmoen 1954 as *Craspedodolbina primitiva* (Verworn 1887). In this species, too, it is impossible to state anything about the ornamentation or the velar morphology without a thorough revision of the original material.

Occurrence.—Tofta Beds: Annelund, Bingers.

Subfamily *Kloedeniinae* Ulrich & Bassler 1923

Fig. 201.

Type Genus.—*Kloedenia* Jones & Holl 1886.

Diagnosis.—*Beyrichiidae* with a long crumina filling out a shallow velar fold and extending from the anterior lobe to the mid-length of the syllobium. The velar edge mostly passes across the crumina, in the female, at least, accompanied by a striate zone or by one or two striate ridges.

Remarks.—Some details of forthcoming studies on the beyrichiid fauna of the *Beyrichia* Limestone and Graptolite Rocks of Northern Germany have to be anticipated here.

Already JONES (1855 a, Pl. V., Fig. 18b) gave a fully identifiable figure of the ventral morphology of *Beyrichia Wilckensiana*, later the type species of *Kloedenia*. The originals are most probably lost (cf. p. 17). The species was correctly identified by KESLING (1956b). This species has been subject to a curious and very far-reaching reduction of the lobation of which only the preadductorial knob, with a characteristic loop, is left, and then very prominent. This species has three ridges ventrally on the crumina.

However, the are about five *Kloedenia* species showing more primitive stages towards the lobal reduction of *Kloedenia wilckensiana*. These species have more or less unreduced syllobia and anterior lobes. The inner ridge on the crumina of the type species proves to originate from a swelling with the typical beyrichiid finger-print striation. The outer ridges originate through a division of the velum.

The shell structure of *Kloedenia* is punctate. Hitherto there is nothing in favour of a development towards or from a reticulation of *Bingeria* type as characteristic of many of those American forms referred to *Kloedenia*. On the other hand, recently published figures definitely confirm that a species very closely related to, or even identical with, the type species occurs in Nova Scotia (COPELAND 1960).

A figure of a female specimen of the generotype *Kloedenia wilckensiana* (JONES), drawn from figures published by KESLING (1956b) is published here to illustrate preliminarily the extreme development in this subfamily. Attention is drawn to the fact that adult tecnomorphs of *Kloedenia wilckensiana* have not been observed. KESLING's figures (1956 b, Pl. VII, figs. 9–11, cf. figs. 1–2) show tecnomorphs belonging to another group of *Kloedenia* species with traces of the normal beyrichiid lobation; the females of these species have a simple striate swelling on the crumina.

Subfamily *Hexophthalmoidinae* n. subf.

TYPE GENUS.—*Hexophthalmoides* n.g.

GENERA.—Only the type genus.

DIAGNOSIS.—*Beyrichiidae* with a small cruminal swelling of unknown genesis occupying the anteroventral part of the valve. Velum with a caudal spine only along a short posterior part of the valve. Lobation dissolved into nodes with cristal loops.

REMARKS.—To give a more complete view of beyrichiacean variation this subfamily and the following forms have to be described or figured. A larger material would probably provide the justification for erecting one or two beyrichiacean families besides the *Beyrichiidae*. These forms probably lived in biotopes otherwise not reached by the present study.

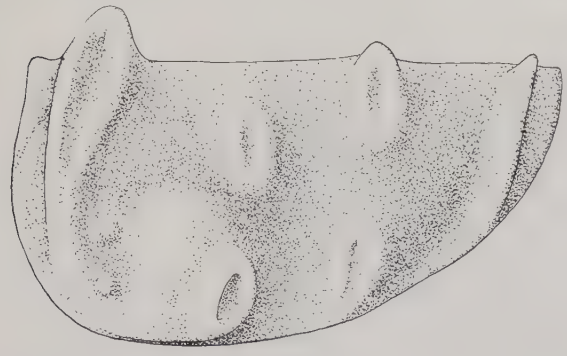


Fig. 202. *Hexophthalmoides* n.g. Drawing based on the holotype of *Hexophthalmoides craterilobatus* n.sp. ×45. Female; tecnomorphs not known from the type locality.

Genus *Hexophthalmoides* n. g.

Fig. 202.

Derivation of the Name.—From Greek ἕξ, six, and ὀφθαλμός, eye, referring to the six cristal loops.

Type Species.—*Hexophthalmoides craterilobatus* n.sp.

Species.—Only the type species.

Diagnosis.—As for the subfamily.

Hexophthalmoides craterilobatus n.sp.

Fig. 203.

Derivation of the Name.—Latin (from Greek) *crater*, crater, and *lobatus*, lobate, alluding to the nodes with cristal loops.

Holotype.—A left female valve, No. G 678 (Fig. 203 A).

Type Stratum and Type Locality.—Hemse Beds at Hammars, Gotland.

Diagnosis.—As for the subfamily and genus.

Description.—Small, longish *Hexophthalmoides* species. The lobal elements are six lobules or nodes. Two of them are the cuspidal parts of the anterior lobe and the syllobium, respectively, and protrude high over the hingeline. Two others are certainly ventral lobules of the same lobal elements, one is the preadductorial node, and the middle ventral node is impossible to place. The velum is a short flange posteriorly, with a short caudal spine. All lobular nodes have cristal loops. The site of the adductor muscles is seen as a shadow.

Provided that the two specimens known are conspecific the crumina causes a considerable downward prolongation of the cristal loop on the cusp of the anterior lobe. The front and middle ventral nodes become incorporated with the crumina but the middle node is still crowned by the cristal loop. The cruminal area between the two loops is occupied by a swelling and a few tubercles.

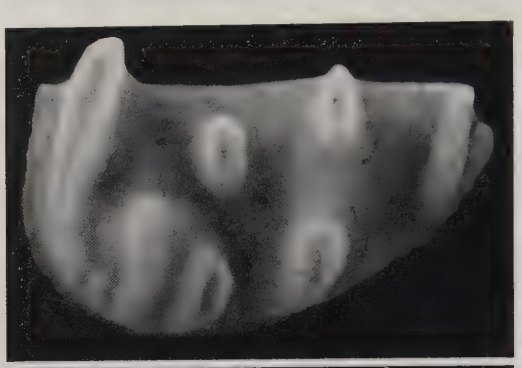


Fig. 203 A. *Hexophthalmoides craterilobatus* n.sp., Hemse Beds, Hammars. Female, No. G 678 (holotype). × 40.

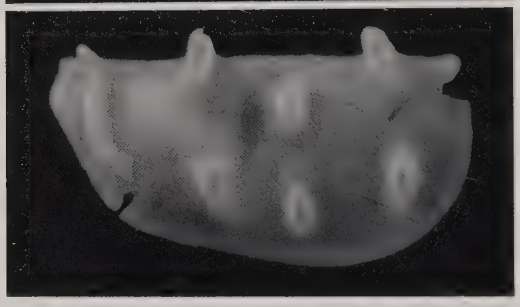


Fig. 203 B. Same species, Hemse Beds, Sigvalde. Tecnomorph, No. G 679. × 40.

The surface of the valve is smooth.

Dimensions.—Hinge length of the holotype 1530 μ, sulcal height 910 μ.

Occurrence.—Hemse Beds: Hammars (one adult female), Tänglings (one adult male).

? Beyrichiacea incertae sedis

Genus *Kolmodinia* n.g.

Derivation of the Name.—Named in honour of Dr. Lars Kolmodin (1843–1905), teacher, ornithologist, inspector of fisheries, archaeologist, and writer of occasional poetry (cf. Munthe 1949), author of the first two small monographs on Palaeozoic ostracodes from Sweden (1869 and 1879).

Type Species.—*Beyrichia grandis* Kolmodin 1869.

Species.—Only the type species.

Diagnosis.—Ostracodes with beyrichiacean-like lobation. There is one tumid anterior element with a characteristic tubercle, one tumid posterior element, two smaller cusps above these lobal elements, and one major cusp between them.

Kolmodinia cf. *grandis*

Fig. 7B.

Remarks.—The large specimen described by Kolmodin (1879) as *Beyrichia grandis* (Fig. 7A) is both fragmentary and distorted. There has been no doubt

that the shell shows arthropode structures, but as the edges of the valve are missing, its bivalve character is not evident in any part of the specimen.

However, a smaller specimen of a closely related, or even conspecific, ostracode has been found in the Eke Beds at Lau Backar. It has the same lobation as KOLMODIN's specimen from Djupvik, but the cuspidal part of the anterior lobe, which is rounded in the specimen from Djupvik, is pointed. The specimen further shows that the posterior lobal unit (a syllobium ?) had a similar cusp, separated as a lobule, and another long, curved lobule along the posterior margin. Between these elements there is another lobal element, more sharply pointed and protruding over the hingeline. A displacement of a preadductorial node into this position is possible, as shown by *Kloedenia*.

The sex of the two specimens is not known. It is not possible to prove that the anterior lobal element is a crumina. If so, the size difference is so large that the specimens can hardly be conspecific. The tubercle on this element is hollow in KOLMODIN's specimen but not so in the new specimen from Lau Backar. These conditions could be due to different factors, from interspecific differences or ontogenetic development to violence sustained during the preparation.

In the new specimen the straight hingeline is preserved. However, there are no details preserved confirming that the species had a hinge mechanism or contact conditions similar to those in the beyrichiids. The state of preservation of the specimen is not good.

The present evidence seems to be sufficient for including the genus among the palaeocope ostracodes. If it can be proved to be a beyrichiacean, which is most probable at present, it cannot be regarded as a beyrichiid but as a representative of a new family.

DIMENSIONS.—Hinge length of the Djupvik specimen ca. 5070 μ, sulcal height ca. 3780 μ. Same dimensions of the specimen from Lau Backar 2830 μ and 1810 μ, respectively.

ADDENDUM

Palaeocope morphology in the "Treatise on Invertebrate Palaeontology", with special reference to the Beyrichiidae

The "Treatise on Invertebrate Palaeontology", Part Q, will unquestionably be used as a standard work by ostracode workers all over the world. As far as the *Beyrichiidae* and associated *Palaeocopa* are concerned, the descriptions and interpretation of morphological features in this study will be found to deviate considerably from those in the Treatise. The parts concerned were already completed when the Treatise appeared, and it has been found more practical, for technical reasons, to summarize the remarks here than to insert them in all those passages where contradictions occur, or to rewrite the text, especially as the views discussed are not very readily accepted. Only some main points can be considered here.

The velum

According to Scott (1961, p. Q 24) the morphological significance of the velum is not clear. This is certainly due to the fact that in the Treatise the velum is confused with another adventral structure, the histium, and that the velum of the *Zygobolbinae* is separated as a new kind of adventral structure, the pseudovelum.

However, Scott (l.c.) adds the important statement that sections of *Beyrichia* show that the velar fold is lined with the inner chitin layer. This must imply that the tubules are lined with chitin inside, which further means that the tubular chitinous lining has been completely isolated from that inner chitinous layer which lined the smooth inner surface of the domicilium; if so, it might have consequences for the hypothesis that the closed tubules can be explained by the retraction or resorption of corresponding epithelial papillae. As this seems to be the first observation of chitin in Palaeozoic ostracodes a more detailed presentation of material and methods behind the statement quoted is desirable.

The Treatise contains contour drawings of new sections through some *Palaeocopa* by J. C. Kraft and J. Wainwright (quoted from Wainwright, J., 1959: Morphology and taxonomy of some Middle Silurian Ostracoda. Urbana 1959; this paper—if printed ?—has not been available). They all show tubuli or velar folds opening towards the domicilium, in an amphitoxotidine (*Beyrichia moodeyi*, op. cit., Fig. 28) and species referred to *Chilobolbina* (op. cit., Fig. 74), *Eurychilina* (op. cit., p. Q 77), *Apatochilina* (op. cit., Fig. 78: 1e), and *Euprimitia* (op. cit., Fig. 78: 9d). It is very possible that more primitive *Palaeocopa* had an open velar fold, or even open tubules, but such hardly existed in normally developed *Amphitoxotidinae*. The enigmatic duplicature found in *Apatochilina* needs, too, some further discussion and explanation.

The cruminal dimorphism

According to Scott & Wainwright (1961, pp. Q 38 – Q 42), the type of dimorphism described in the present study and regarded as closely related to the velar dimorphism, consists of two fundamentally different kinds of dimorphism, called the *lobate* (i.e. *lobal*, cf. p. 72) and *beyrichiid* dimorphism, respectively. All examples of the former kind of dimorphism are *Zygobolbinae*. It is stated that the lobes (i.e. the cruminae) referred to show no evidence of a remnant partition as *always* (italics here) is found in *Beyrichia* (reference is then made to op. cit., Fig. 27 where it is shown that *Beyrichia*, s.l., in contrast to the *Treposellinae*, does not have a partition but only some thickening in the area where the inflation of the crumina has caused a sharp, ring-shaped bend in the carapace wall).

Scott & Wainwright (op. cit., p. Q 41) confirm the statement by Swartz

(1936; cf. p. 216 herein) implying that the crumina is formed by an inflation of the epidermal fold that produced the velum. This is somewhat simplified truth as far as the *Amphitoxotidinae* is concerned; in the other subfamilies the procedure is more complicated. The simple inflation of the crumina is, among the subfamilies investigated hitherto, probably best realized in the *Beyrichiinae*, by reduction of the dolonoid apparatus and incorporation of valve wall elements; in the *Kloedeniinae* the occupation of the velar fold looks still more simple in external view; it is not quite improbable, however, that sections or internal preparations may surprise in this respect. *Kloedenia* is being studied from this point of view.

Scott & Wainwright (op. cit., p. Q 41, cf. p. 108 herein) in this connection adopt Kesling's views as to the phylogenetical and chronological importance of an encroachment of the unspecialized parts of the velum onto the crumina.

Scott & Wainwright (op. cit., p. Q 41) draw a line of cruminal development over *Velibeyrichia moodeyi* and *Macrypsilon salterianum* to *Phlyctiscapha* in order to show a prevailing tendency of the beyrichiids toward separation of the cruminal cavity from the domicilium, in cases accentuated by the presence of a dividing wall. On the contrary—and the *Treposellinae* are in this respect a fairly primitive exception—the beyrichiids show a very marked tendency towards simplification of the crumina and even of the unspecialized velum.

Both in advanced *Beyrichiinae* and in the *Zygobolbinae* the cruminae open very widely towards the domicilial space, without the proximal constriction which has given the impression that the beyrichiids tend to develop a dividing wall in this region. The velum in *Zygobolba* is far better developed than in any *Beyrichiinae*, and the crumina is also far more primitively velar in origin in *Zygobolba*. The cruminal development within different zygobolbine genera, however, needs more study; it is not impossible that some of them reached the developmental level of the *Beyrichiinae*.

Without respect to the relative rank given to the taxionomic units in the Treatise (subfamilies in this study would be families there) there is no basis for distinguishing the *Zygobolbidae* as a special family if the other *Beyrichiidae* are kept together in one unit. The *Craspedobolbininae* and *Amphitoxotidinae* are, then, relatively more distantly related to *Beyrichia* than is *Zygobolba*.

General morphological and classificatory conclusions

Adventral structures appear in the *Palaeocopa* but are very frequently reduced. If a velum is present it is not always dimorphic. There are even cases within the *Beyrichiidae* where the velum has become obsolete but where a carapace dimorphism, phylogenetically of velar origin, clearly persists.

In the morphological and classificatory treatment of the *Palaeocopa* we cannot make the grouping of species and genera mechanically dependant on the absence

or presence of adventral structures, a certain lobation, or dimorphism. If one of these features is absent—undeveloped or reduced—the other features are generally sufficient to place the animals into a complex or a line of homologies showing their true relationships. However different the typical cruminal dimorphism or the extreme histial—the locular—dimorphism may seem to be in comparison with simply velate forms, the obvious homologies in lobation and in the mere existence of a dimorphism in any way preponderantly associated with the anteroventral part of an adventral structure must encourage us to search for a not too distant common origin. Both phylogenetic and ontogenetic methods are available for this.

Unfortunately the splitting of the *Hollinacea* and the splitting and regrouping of the *Eurychilinacea* in the Treatise follow other norms of classification which do not allow the establishment of homology chains of this kind. However, during the last decade systematic studies have been published which from different points of view illustrate the position of the *Beyrichiidae* among the Palaeocopa (Jaanusson 1957) and the *Palaeocopa* among the *Ostracoda* (Pokorný 1953; the suborder name *Palaeocopa* introduced by Henningsmoen 1953). For this purpose the main features in a palaeocope system have been surveyed as an introduction to the descriptive part of this paper.

A new term leading to confusion is *pseudovelum*, a "frill-like marginal or submarginal rim comprising single layer of shell, not compressed double-layered outfolds of valve walls." Scott (op. cit., p. Q 24; cf. above, p. 356) uses it for the typical dimorphic velum of *Zygobolba* but also for the flange-like structure in many "*Drepanellidae*" (op. cit., p. Q 84). It is true that reliable evidence for the homology of, e.g., the neodrepanelline flange with the velum is still lacking, but a new term to illustrate this seems unnecessary.

In earlier terminology the marginal structures have always been associated with the *free margin* and are defined accordingly in the Treatise (p. Q 52, Figs. 16, 19, and 20). Scott, however, uses it also for adventral structures separated from the marginal region, such as the velum and the histium, which leads to statements such as "The Drepanellacea are separated from Hollinacea because they are non-dimorphic, and as such, lack the marginal structures so characteristic of the latter group" (op. cit., p. Q 84). In the recent ostracode suborders it is of minor importance whether *free margin* and *margin* (=lateral outline, sometimes border) are confused; in the Palaeocopa it is better to reject the latter term in favour of *lateral outline*. It is quite necessary, however, to refer the marginal structures, which are non-dimorphic, and the velum and histium, which can exhibit dimorphism, to two different groups of structures at different distances from the free margin. Particularly in the central palaeocope superfamilies they are morphologically very similar. Here both groups have been called adventral (cf. p. 72).

According to Scott (op. cit. p. Q 82) some representatives of the palaeocopids "show no evidence of dimorphism and may have reproduced parthenogenetic-

ally". On the contrary, it is possible to infer parthenogenesis only in dimorphic species, and then only where the heteromorphs constitute 100%, or very slightly less, of the adult specimens.

Stratigraphical distribution of the Beyrichiacea

All ostracodes at present known with certainty to be beyrichiids are Silurian or Devonian. MOORE (1961, Figs. 35 and 47) states a time range for the *Beyrichiacea* from the beginning of the Middle Ordovician into the Early Permian. There remain many unrevised statements in older literature (almost entirely covered by BASSLER & KELLETT 1934) on which the tables quoted are probably based. All references to *Kloedenia* and *Zygobolba* are believed to have been checked here in this respect. None of the pre-Silurian forms referred to these genera are beyrichiaceans. The youngest *Kloedenia* (s.str.) finds checked are Downtonian (Ludford Corner, Ludlow, about 120 cm above the Ludlow Bonebed). The genus *Nodella*, referred to as a Late Ludlovian zygobolbid, is placed in the *Drepanellidae* by SCOTT in the current text; it is not a beyrichiacean. *Tribolbina*, finally, ranging through the Mississippian and Pennsylvanian into the Early Permian, is not a beyrichiacean genus (references to North American material not checked).

The anglicized form of *Ostracoda*

It is welcome that an editorial statement has been made in the Treatise as to the correctness of the spelling *ostracode* (p. Q 2).

Discussions as to this important detail are legion among ostracode workers. Standard English adopts the Greek suffix -ώδης exclusively as *-ode*, and the spelling *ostracode* is the only one recognized by the current editions of the Oxford Dictionaries. As pointed out in the Treatise, the American Webster Dictionary recognizes both *ostracode* and *ostracod*. This seems to be the only case among the several familiar scientific terms (*geode*, *phyllode*, sometimes *staminode*, etc.) derived from -ώδης in which an ending *-od* occurs (probably erroneously influenced by *-pod* in *phyllopod*, *brachiopod*, etc.). In those rare cases where the same author uses *ostracod* together with one of the other words (WELLER 1960, LAHEE 1961, *geode*) this is nevertheless spelled with *-ode*. In *geode*, *phyllode*, etc., the *o* is a diphthong in both standard and American English. The spelling *ostracod* has so little basis in analogy with other terms based on -ώδης and in the pronounciation of this ending as adopted into English that it must be stamped as wrong.

The beyrichiid faunas of Siberia

In a recent paper ABUŠIK (*in* ABUŠIK, IVANOVA, KOČETKOVA, MARTYNOVA, NECKAJA, & ROŽDESTVENSKAJA 1960) describes a series of new beyrichiids from the Silurian of Siberia. Especially interesting is the new, non-lobate genus *Moierina* (Early Ludlovian) with a crumina like that of *Bolbibollia*, incorporating

much of the carapace wall. Its craspedobolbinine nature cannot, however, be definitely established on the basis of the figures published. An interesting beyrichiine, Llandoverian in age, is described as *Beyrichia* (*Beyrichia*) *aspera* Abušik. It has a cuspidal, apparently cristate, plica on the syllobium, foreign to all other beyrichiines, and a crumina which incorporates less of the carapace wall than any other representative of the subfamily. The zygal region is entirely unaffected, but there is no distinct zygal arch in either dimorph. *Beyrichia* (*Mitrobeyrichia*) *kureikiana* Abušik can hardly be a craspedobolbinine. Two interesting Llandoverian forms are the *Slependia*-like *Plethobolbina dorsicostata* Abušik and *Beyrichia* (*Velibeyrichia*) *patagium* Abušik; unfortunately the figures do not allow any definite conclusion as to their systematic positions.

A study of the Llandoverian beyrichiid faunas may probably result in the discovery of interesting primitive stages in the phylogeny of the crumina in branches other than the craspedobolbinine. All the best possibilities of finding lower parts of the Llandoverian in a facies convenient for the preservation of beyrichiids are confined to the area of the U.S.S.R. The incomplete Llandoverian sequence below Gotland, as far as is known from preliminary investigation of existing cores, is not very promising in this respect.

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